



AN ABSTRACT OF THE THESIS OF

Mark F. Raggon for the degree of Master of Science in Fisheries Science  
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Title: Seasonal Variability in Diet and Consumption by Cottid and Salmonid  
Fishes in Headwater Streams in Western Oregon, USA

Abstract approved:

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Coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) and cottids (*Cottus* spp) commonly co-occur in headwater streams in western Oregon. Little is known about the comparative trophic ecology of these species or how they respond to seasonal scarcity of resources. In this study I evaluated the seasonal variability in diets and consumption as it related to food limitation for coastal cutthroat trout and cottids. Over 340 individual diets were quantified from seasonal samples collected in May, July and September of 2008. Diet overlap was relatively low among seasons and species. Coastal cutthroat trout exhibited a more diverse diet in terms of taxonomic richness of prey and consumed both aquatic and terrestrially-derived prey, whereas cottids appeared to specialize on aquatic prey. Based on diet composition and amount consumed, all species appeared to be increasingly food limited from July to September, relative to May.

However when diet composition was integrated with a bioenergetic model, coastal cutthroat trout were found to be substantially more food limited than cottids. Differences in the cost of activity between these species may explain this result. Activity costs may be higher for trout, which reside in the water column and rely on active swimming, versus cottids, which lack a swim bladder and are more benthic oriented. Results of this work suggest that cottids are dietary specialists, feeding almost exclusively on benthic prey, whereas coastal cutthroat trout utilize a much broader resource base. In spite of this, bioenergetic models suggest cottids fare better during periods of resource scarcity in headwater streams. Overall, this suggests it is important to look beyond simple indicators of individual performance, such as directly observed consumption or growth. Intense food limitation, especially for coastal cutthroat trout, may have important implications for individuals, populations and species interactions during low flow conditions in streams in western Oregon.

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Seasonal Variability in Diet and Consumption by Cottid and Salmonid Fishes in  
Headwater Streams in Western Oregon, USA

by  
Mark F. Raggon

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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Mark F. Raggon, Author

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## CONTRIBUTION OF AUTHORS

Dr. Jason B. Dunham was involved in the study design, data analysis and editing of all sections of this manuscript. David Hockman-Wert provided the map of stream locations in Chapter 2 and assisted in database management.

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## **CHAPTER 1 – GENERAL INTRODUCTION**



The question of bottom-up or top-down control of food webs addresses whether predation (top-down) or abundance of resources (bottom-up) determines energy flow and ultimately influences how fitness of individuals scales up to population and community dynamics (Hairston et al. 1960; Power 1992). Bottom-up control of food webs occurs when energy flowing up from the base of the food web through successive trophic levels is limited by abiotic factors (e.g., light, nutrients) influencing primary production and energy transfer to higher trophic levels (Hairston et al. 1960, Fretwell 1987, Oksanen 1991). Top-down control differs in that consumers at the top of the food web are resource limited and production at lower trophic levels alternates between being limited by predators and resources (Hairston et. al. 1960, Bowlby and Roff 1986, Fretwell 1987, Oksanen 1991). Long-term research on food webs in river ecosystems has shown the importance of these processes can vary both seasonally and among years. For example, stream discharge in particular appears to be a major physical influence on food webs over time as fundamental relationships between predators and prey are strongly influenced by the previous winter's flood regime (Power et al. 2008). Food webs may reassemble from year to year during the summer low flow period based on the presence or absence of bed-scouring flood events removing (or leaving) accrued algae from the previous summer. Subsequently, production of different macroinvertebrate types (e.g. colonizers, grazers) may vary in their availability to fish predators.

As a result of macroinvertebrate types potentially varying seasonally and among years (or locations), patterns of predation by fishes and other top consumers may vary and complicate application of traditional top-down and bottom-up models (Hargrave et. al. 2006, Cheever and Simon 2009). In spite of these complexities, these simple models of energy flow within food webs do provide a useful framework for proposing hypotheses and predictions about fundamental processes driving food webs (Carpenter and Kitchell 1993). Identification of critical processes influencing structure of food webs may be most evident during seasonally shifting abiotic (e.g., light, temperature, nutrients) and biotic (e.g., consumer and prey abundances) conditions within streams when food may become limited, providing the necessary template to examine how seasonal changes in food webs relate to responses in fish predation patterns (McQueen et al. 1989, McIntosh et al. 2005).

Seasonal changes in processes regulating food webs within stream ecosystems are well known (Nakano et al. 1999, Nakano and Murakami 2001, Baxter et al. 2005). Responses of predators to seasonal changes in prey availability or abiotic (e.g. low-flow, decreased habitat) conditions in streams may have important consequences for the prevalence of top-down or bottom-up processes in food webs. Furthermore, the degrees to which different consumers exploit or compete for resources during seasonal events based on their respective

morphological and or behavioral characteristics (Connell 1980) may dominate top-down or bottom-up processes – creating a consumer-mediated system.

As a major part of the fish fauna in headwater streams of the Pacific Northwest, salmonids (family Salmonidae) and cottids (family Cottidae) exhibit different morphological and behavioral adaptations to forage in lotic systems (Reeves et. al. 1998). Salmonids primarily forage in the water column on drifting invertebrates (both terrestrial and aquatic) and on the benthos, relying on visual cues to locate and capture prey (Ware 1973). In contrast, cottids spend almost all of their time on the stream bed, feeding on benthic invertebrates (Dineen 1951, Mann & Orr 1969, Li & Moyle 1976).

To examine the importance of seasonal influences associated with low flows, changes in prey types, and food limitation in headwater streams, I compared the patterns of predation between coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) and a guild of cottids consisting of three species (*Cottus asper*, *Cottus perplexus*, *Cottus gulosus*). My goal was to investigate how these predators responded to seasonal shifts in prey assemblages in headwater streams in western Oregon to evaluate food limiting conditions experienced by these fish. In these rain-dominated flow systems, stream flows may decline in summer and early fall as water temperatures increase. These changes, combined with increased numbers of fish via recruitment from spring spawning, may lead to increased resource limitation and competition within and among these species in

summer and early fall. I assessed whether these events associated with this “ecological crunch” period (Wiens 1977) in western Oregon headwater streams were associated with responses in the predation patterns of coastal cutthroat trout and cottids, and whether they were food limited based on unique characteristics of species’ morphology, behavior, and physiological characteristics (bioenergetics).

**CHAPTER 2 - SEASONAL VARIABILITY IN DIET AND  
CONSUMPTION BY COTTID AND SALMONID FISHES IN  
HEADWATER STREAMS IN WESTERN OREGON, USA**

## Introduction

The faunas of Pacific Northwest headwater streams are often dominated by fishes from two families, family Cottidae (cottids or sculpins) and family Salmonidae (salmon, trout, charr, and relatives; Berra 2001). Whereas salmonids are very well studied (Crisp 2000, Quinn 2005), cottids are considerably less well known (Adams and Schmetterling 2007). Cottids can be very abundant in some systems; perhaps more so than co-occurring salmonids in many cases (Beauchamp 1990, Cyterski and Barber 2006). In addition to their abundances being different, their methods of foraging are as well. Salmonids primarily forage in the water column on drifting invertebrates (both terrestrial and aquatic) and on the benthos, relying on visual cues to locate and capture prey (Ware 1973). Cottids are more benthic oriented and believed to forage primarily on benthic invertebrates (Dineen 1951, Mann & Orr 1969, Li & Moyle 1976). Cottids and salmonids co-existing in lotic systems have been known to consume similar prey (Ruetz et. al 2003, Hesthagen et. al 2004) despite their disparate foraging techniques; however investigations into whether they are interacting for prey items have yielded ambiguous results.

Studies of ecological interactions between salmonids and cottids are limited in number, but reveal a great deal of complexity. For example, a study utilizing stream enclosure experiments found growth of large cottids to be reduced in the presence of nonnative brown trout *Salmo trutta*, but not in the

presence of native brook trout *Salvelinus fontinalis*, even though there was no traceable difference in the diet composition or invertebrate availability between treatments (Zimmerman and Vondracek 2007). Other studies have shown that cottids may prey extensively on the eggs and larvae of other fishes under experimental settings (including salmonids; Tabor et. al. 2004, Tabor et. al 2007). Brocksen et. al. (1968) showed in a laboratory study cottids were capable of cropping benthic invertebrate stocks, subsequently reducing the amount of prey potentially available to drift-feeding salmonids. Although most cottid/salmonid studies address interactions for prey, other experimental studies have shown cottids are capable of displacing salmonids to less preferred habitats composed of finer substrates (Hesthagen and Heggenes 2003). The relative strengths of these interactions may also vary based on the amount of intraspecific competition occurring between cohorts of the same species (Grossman et al. 2006). The outcomes of intraspecific interactions typically preclude interspecific interactions, influencing the degree to which interspecific interactions take place. Furthermore, the degrees to which different consumers exploit or interact for resources can also be a function of their respective morphological and or behavioral characteristics (Connell 1980).

Although cottids and salmonids differ in their morphological characteristics (e.g. gape, body shape), their diets have been found to overlap to a

degree considered biologically significant (Hesthagen et. al 2004). Early studies of interactions between cottids and salmonids found that both species would prey upon one another while also eating similar benthic invertebrates, acting as predators and competitors with one another (Moyle 1977) suggesting the two species could be operating as a single guild -- intraguild predators (Polis and Holt 1992). Due to the multitude of interactions between cottids and salmonids observed, interpretations about the ecological importance of these interactions have been difficult to synthesize. Furthermore, current literature has not addressed how cottid and salmonid interactions relate to the seasonality of the food webs they occupy. Processes associated with seasonality in streams, such as how species respond to resource limitation, environmental variability and predation has been shown to be a critical factor in structuring fish assemblages (Connell 1978, Grossman et. al. 1982).

To evaluate the potential importance of seasonal variability and food limitation within aquatic food webs, I studied co-occurring coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) and a trophic guild of cottids (*Cottus asper*, *Cottus perplexus*, *Cottus gulosus*) in western Oregon headwater streams. Given that the importance of biotic interactions can be highly seasonal in this region, I conducted my work from spring through early fall to account for the potential role of seasonality in observed responses. Flows in these streams are characterized by



a rain dominated hydrograph that produces high and flashy winter flows, followed by a protracted season of low flow in summer and fall (Harr 1976, Ziemer and Lisle 1998). These low flows, combined with recruitment of juvenile cottids and salmonids in summer (Reeves et al. 1998) can lead to high densities of individuals. Low flows and recruitment also coincide with the onset of warmer water temperatures and decreased aquatic prey availability (Hershey and Lamberti 1998). This series of events suggests a progression of increasing aquatic resource scarcity (Wiens 1977) starting with relatively abundant prey in spring, followed by increasingly limited availability in summer through fall, prior to fall freshets (Gasith and Resh 1999).

The seasonal nature of streams and biota has important implications for structuring interactions within and between species. From the perspective of species with flexible foraging strategies (salmonids) versus potential benthic specialists (cottids), it is more likely the latter will suffer from declines in aquatic productivity. This is because salmonids may be more able to utilize terrestrially derived prey, which can be more abundant in summer and fall (Wipfli 1997, Nakano et al. 1999, Nakano & Murakami 2001, Baxter et. al 2005). Increases in availability of terrestrial prey may not be enough however to offset other low-flow constraints on salmonids; recent work suggests that survival of coastal cutthroat trout is at a minimum during summer and fall low-flows, but the specific

processes at play (e.g., starvation, predation, or interactive effects) are not clear (Berger and Gresswell 2009). In this study I sought to further understand the importance of food limitation for both cottids and salmonids during a hypothesized season of relative resource abundance (spring) to relative scarcity (fall).

Within each season (spring, summer, early fall) I quantified seasonal differences in the diet composition and consumption rates of coastal cutthroat trout and cottids. I further examined how those responses in diet related to the physiology of both consumers as revealed by bioenergetics models (Hanson et al. 1997). I predicted differences between cottids and coastal cutthroat as follows:

- 1) cottids, because of their suspected larger gape sizes would be less gape-limited compared to coastal cutthroat trout and consume larger prey taxa; and there would be
- 2) low diet overlap between cottids and coastal cutthroat trout resulting from the differences in foraging behavior between these two species (Moyle 1977); and
- 3) higher consumption rates of aquatic macroinvertebrates by benthic oriented cottids because they have greater access to these prey compared to water column dwelling coastal cutthroat trout; and
- 4) higher consumption rates of terrestrially derived drift by coastal cutthroat trout because of greater access to these prey in the water column relative to benthic oriented cottids. I expected seasonally shifting conditions of prey and habitat availability due to influxes of terrestrial

invertebrates, low flow conditions (decreased habitat, less space for individuals), and increased fish densities due to emergence of young-of-year and temperature increases. Accordingly I predicted the following seasonal influences on diet: 1) increasing divergence of diets (lower overlap) between cottids and coastal cutthroat trout from spring through fall as terrestrial prey become a more prominent resource for trout, 2) lower richness in prey consumed by cottids relative to coastal cutthroat trout as aquatic macroinvertebrates are suspected to be less abundant in summer and early fall and terrestrial prey become more available to coastal cutthroat trout; and 3) increased food limitation and decreased growth efficiency for cottids relative to coastal cutthroat trout as aquatic prey become less available through summer and fall.

## Methods

### *Study area*

This study was conducted in the Trask River basin, which drains a major portion of the northern Oregon Coast Range (Figure 2.1). Four stream sections within the Trask River basin were used as study sites. Elevation of all four sites ranged from 324 m to 608 m (Table 2.1). The underlying geologic formations consisted of marine sandstones and shale, with basaltic volcanic rock (Franklin and Dryness 1988). The upland forest near the stream sections were mainly composed of Douglas fir (*Pseudotsuga menziesii*), whereas riparian zones were populated by deciduous species including red alder (*Albus rubra*), big leaf maple

(*Acer macrophyllum*), vine maple (*Acer circinatum*), and salmonberry (*Rubus spectabilis*). Climate in this system is defined by mild, wet winters (October – June) and cool, dry summers (July – September; Spies et al. 2002). Annual precipitation ranges from 150 to 500 cm and falls mostly as rainfall with snow restricted to the higher elevations during November, December, and January (Nolin and Daly 2006). All sites within the basin were restricted to the headwater areas near the upper extent of fish distribution. Species present within the basin included coastal cutthroat trout (*Oncorhynchus clarkii clarkii*), coho salmon (*Oncorhynchus kisutch*), rainbow/steelhead trout (*Oncorhynchus mykiss*), prickly sculpin (*Cottus asper*), reticulate sculpin (*Cottus perplexus*) and riffle sculpin, (*Cottus gulosus*). Cottids tended to be the most abundant species in the Trask watershed (J. Dunham and D. Bateman, personal communication).

## Trask River Watershed Study

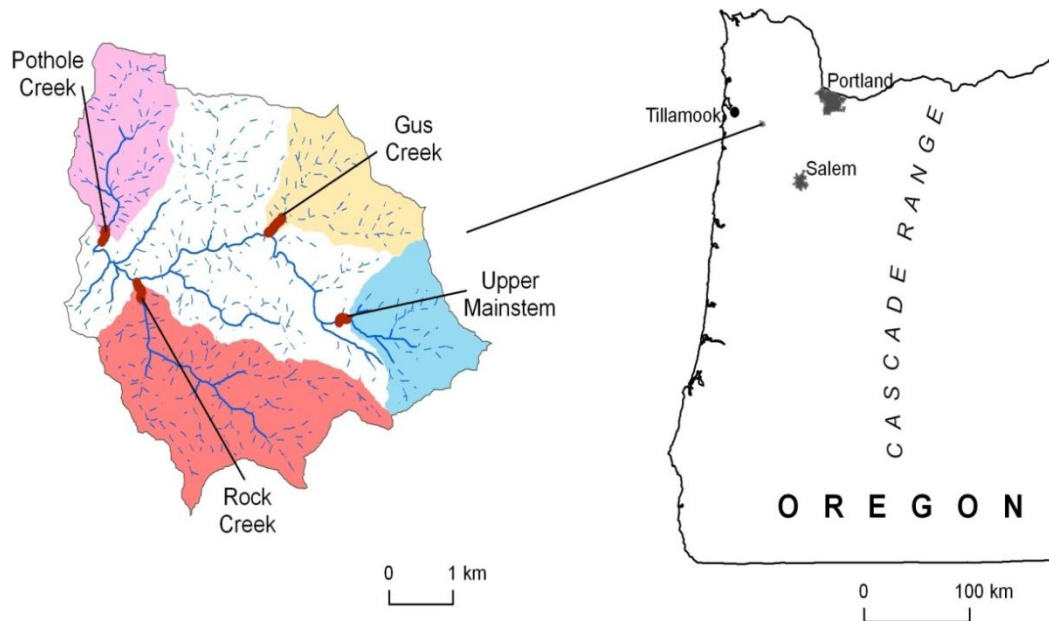


Figure 2.1. Names and locations of the four stream sites within the Trask watershed.

Table 2.1. Characteristics of stream sections within the Trask watershed; stream name, elevation of site, site length, mean daily temperature and species present.

Stream	Elevation (m)	Site Length (m)	Temperature (C)	Species Present
Pothole Creek	324	211	11.1	CT, RB, PSC, RFS, CO
Rock Creek	335	277	11.6	CT, RB, PSC, RFS, CO
Gus Creek	463	297	11.7	CT, RFS
Upper Mainstem	608	183	10.8	CT, RFS

CT = coastal cutthroat trout, RB = rainbow trout, PSC = prickly sculpin, RFS = riffle sculpin/reticulate sculpin, CO = coho salmon

#### *Fish sampling*

Fish were captured by backpack electrofishing in May, July and September 2008. During initial capture of coastal cutthroat trout and cottids, individuals were measured (fork length for trout and standard length for cottids; nearest 1 mm) and weighed with a digital balance (nearest 0.1 g). Individual fish greater than or equal to 100 mm in length (mostly coastal cutthroat trout) were implanted with a 23 mm half duplex passive integrated transponder (PIT) tags. Individual fish less than 100 mm in length were injected with 8.5 mm full duplex PIT tags. After May, stream sections were re-sampled in July and September in attempts to recapture previously PIT tagged coastal cutthroat trout and cottids to quantify the change in mass (grams) required for bioenergetic modeling input.

*Sampling of fish diets*

The minimum size of fish sampled for diet across all species was 55 mm standard (SL) for cottids or fork length (FL) for salmonids. Coastal cutthroat trout were partitioned into size classes less than and greater 100 mm FL to evaluate anticipated differences in the patterns of predation between relatively older, larger cutthroat versus smaller, younger fish. I attempted to sample at least 40 individual diets (stomachs) for each species and or size class per season (hereafter referred to as consumer class). To sample diets for examination of stomach contents, fish were collected by sampling upstream with backpack electrofishers in May (20-22), July (26-29), and September (17-19), 2008. The goal was to sample each stream (4) until at least 10 coastal cutthroat trout < 100 mm, 10 coastal cutthroat trout  $\geq$  100 mm and 10 cottids had been collected. Collection of diets occurred between 8:00 and 17:00 to include stomach contents of both terrestrial and aquatic prey. Stomach contents were sampled using gastric lavage (Giles 1980). At the time of capture the date, site, time, species, length and weight were recorded on a piece of Rite in the Rain<sup>®</sup> paper along with the stomach contents (preserved in 95% ethanol entrapped in a coffee filter) and placed into a Whirl Pack<sup>®</sup> bag.

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### *Laboratory processing of fish diets*

In the laboratory, prey organisms in fish diets were taxonomically identified to either the family (most cases) or order (when individuals were partially digested and difficult to identify) using a dissecting microscope. Prey taxa were classified based on origin (aquatic or terrestrial). Prey size was quantified using an ocular micrometer. Individual invertebrates were measured to the nearest 0.5 mm in length for wholly intact invertebrates while the head widths were measured to the nearest 0.5 mm for partially digested invertebrates. These lengths and head widths were used to determine individual macroinvertebrate biomass using published taxon-specific length-mass and head-length regression equations (Hodar 1996, Benke et. al 1999, Sabo 2002). I used these equations to document seasonal changes in the biomass of ingested aquatic and terrestrial prey and to calculate diet proportions for bioenergetic modeling.

### *Consumer similarity*

To account for potential difference in cottid and coastal cutthroat diets I measured differences in gape sizes from preserved specimens from the Oregon State University Fish Collection. I used digital calipers to measure gape as the transverse distance across the corners of the mouth when closed. Measurements were recorded to the nearest 0.1 mm. Furthermore, I evaluated whether species may be potentially gape-limited by comparing the head widths of invertebrates consumed (Bozek et. al 1994).



Cottids and coastal cutthroat trout consuming similar prey taxa indicates sharing of resources but an overlap index quantifies the level of similarity in their respective diets. Since cottids are considered to be specialized benthic predators terrestrial prey taxa were excluded from diet overlap analysis. Results of this work (reported below) supported this assumption. To evaluate how cottids and coastal cutthroat trout seasonally overlapped in their consumption of aquatic macroinvertebrates during May, July and September, I used the Morisita's index of diet overlap for prey counts (Smith and Zaret 1982). Values of this index range from 0 to 1, representing zero to complete overlap. The degree of diet overlap is considered to be biologically significant only when the index is greater than 0.60 (Wallace 1981).

*Food limitation: direct observation*

I compared the relative differences in the consumption rates (mg of prey/gram of fish) of aquatic and terrestrial derived prey between consumer classes within seasons and among seasons to evaluate whether consumers were food limited relative to each other. Diet richness is a useful measure to evaluate whether consumers are consuming a number of different taxa or are restricted (or specialized) to consume a smaller quantity. To quantify the breadth of aquatic macroinvertebrate consumption by cottids and coastal cutthroat trout I used species-richness curves modified as family-richness curves as I only identified individuals to the family level. Prior to diet richness comparisons being made, I

used rarefaction (EcoSim Version 7.72; Gotelli and Colwell 2009). Rarefaction addresses the simple but often overlooked aspect that, as more individuals or samples are accumulated more families will be recorded (Gotelli and Colwell 2001). Thus, it is important to control for unequal numbers of individuals when comparing species richness between samples. I also evaluated potential differences in diversity of diets by examining how the contribution of taxonomic orders varied across seasons and consumer classes by calculating the mean diet proportions of Ephemeroptera, Plecoptera, Trichoptera, Diptera, Coleoptera and Hymenoptera orders.

*Food limitation: bioenergetics*

I used the Wisconsin bioenergetics model (Hanson et al. 1997) parameterized for rainbow trout (*Oncorhynchus mykiss*) and prickly sculpin (Moss 2001) to evaluate how responses in growth and predation patterns related to seasonal changes in prey types (reflected in different energy densities of prey), thermal regimes and body size of consumers. Although parameters for each consumer in my system were often adapted from different species (e.g., substitution of *O. mykiss* for *O. clarkii*, and equal parameters for all cottids), I assumed this did not influence outcomes of the analysis in terms of comparing species in different families (Salmonidae versus Cottidae). For this aspect of the study I focused bioenergetic modeling to the July-September period due to the lack of recaptured fish in July from fish tagged in May. I used continuous

seasonal temperature data (recorded at one hour intervals and summarized in terms of daily means) from the four stream sites to evaluate how temperature affected growth within this timeframe (data provided by Maryanne Reiter, Weyerhaeuser Company, and Arne Skaugset, College of Forestry, Oregon State University). In addition to temperature, diet proportions are required for model input. Diet proportions were calculated by using biomass estimates of terrestrial and aquatic invertebrates that were binned as either; soft larvae, rigid larvae, aquatic nymph, aquatic adult, Coleopteran, Hymenoptera and terrestrial invertebrates, with a specific energy density value assigned for each (McCarthy et. al. 2009; Table 2.2). Dry weights of prey were for each prey category and then converted to wet weights for diet proportions (Lowery 2009). I used the mean proportion by weight ( $MW_i$ ) instead of the pooled proportion by weight ( $W_i$ ) to calculate diet proportions, because  $MW_i$  is considered to be a more representative measure of diet and is less susceptible to bias produced by rare, large prey taxa consumed as a result of opportunistic feeding events (Beauchamp et. al 2007).  $MW_i$  estimates the diet proportions for individual stomachs first and then these proportions are averaged across all non-empty stomach samples. In contrast,  $W_i$  is an estimate of average diet proportions by weight when all gut contents are pooled.

From these model inputs I estimated seasonal consumption rates for individual cottids and coastal cutthroat trout by using individual growth rates based on the number of recaptured fish from July to September from the four stream sections. To better understand how consumption rates related to growth, I divided the incremental weight gain (or loss) by the modeled consumption rate to estimate growth efficiency (GE). To evaluate the prevalence of food-limiting conditions experienced by individual fish, the estimated consumption  $C$ , computed by the model was reported as a  $P$ -value ( $P=C/C_{\max}$ ), the proportion of maximum consumption expected for individual fish after accounting for the effects of body mass and water temperature.

Table 2.2. Energy density values used for bioenergetic modeling based on prey type (McCarthy et. al 2009).

Prey type	Energy Density (J/g)
Aquatic larvae, soft bodied <sup>a</sup>	2,746
Aquatic larvae, rigid body <sup>b</sup>	4,272
Aquatic nymphs <sup>c</sup>	3,076
Aquatic adults <sup>d</sup>	4,224
Coleoptera adults	6,387
Hymenoptera adults	5,133
Other Terrestrial invertebrates	5,500

<sup>a</sup>Diptera (Cummins and Wuycheck 1971)

<sup>b</sup> Coleoptera and Trichoptera.

<sup>c</sup> Ephemeroptera and Plecoptera.

<sup>d</sup> Ephemeroptera, Plecoptera, Trichoptera and Diptera.

### *Statistical Analyses*

To test for differences between gape sizes between preserved specimens, I used Analysis of Covariance (ANCOVA) with standard length (mm) as a continuous variable for both cottids and coastal cutthroat trout. Data were log transformed (base 10) to account for unequal variances among gape sizes as body length increased. Examination of residual plots and Levene's Test for equality of variances revealed a pattern of increasing residual variance with increasing body size.

Analysis of variability in bioenergetic parameters began with an assessment of the redundancy of model outputs: overall consumption (C), growth efficiency (GE), and relative consumption ( $P$ -value or  $C/C_{max}$ ). Correlation analyses revealed these measures to be highly redundant (Appendix A), indicating each would produce similar statistical comparisons between consumers. For further analyses, I considered  $P$ -value to be the most biologically important measure of food limitation (McCarthy et. al. 2009). Variability in  $P$ -values within and among seasons for each consumer class and among consumer classes in each season was analyzed using the non-parametric Kruskal-Wallis (KW) one-way analysis of variance.

## Results

Of the 343 stomach contents collected, 17 stomachs were empty, resulting in 326 non-empty stomachs available to determine diet composition and biomass of ingested prey. The maximum number of empty stomachs for any consumer class was low and occurred in September for cottids ( $n = 3$  of 36 individuals handled). This suggested most fish during this study were actively or had recently been foraging within the time of capture (0800 – 1700). Evidence of piscivory was only found in the stomach contents of two cottids, which contained unidentified fin and scale fragments. During May due to high water conditions field sampling of cottids and large cutthroat trout proved to be challenging and resulted in lower than desired numbers of diets being sampled (< 40 individuals, Table 2.3).

All sites and subsequent analysis were pooled during each season due to the large variations in the numbers of species collected by site among and within seasons (Appendix B-1). While this may have contributed to increased variance within our results by omitting site-site variation, I was more interested in the question of variability among consumer classes through time (i.e., season), not space (i.e., sites).

Table 2.3. Summary of non-empty stomachs collected for small coastal cutthroat trout (CT < 100 mm), large coastal cutthroat trout (CT > 100 mm) and cottids during May, July and September 2008 within the Trask watershed.

Consumer class	May	July	September
CT < 100 mm	42	38	39
CT > 100 mm	24	39	36
Cottids	27	48	33

### *Consumer similarity*

Most cottids captured were less than 90 mm SL with only a few larger individuals observed. Therefore inclusion of specific coastal cutthroat trout size classes was scaled to suit the common size classes of cottids. I measured 50 individuals per species ranging from 50 to 100 mm SL. Gape widths tended to be positively related to body length for all species (Figure 2.2). Gape widths among all species were statistically different (ANCOVA:  $df = 3$ ,  $F = 125.29$ ,  $p < 0.001$ ). Levene's test for equality among variances revealed increasing variance of gape widths as body length increased. Statistical inferences were complicated due to the unequal variances at different body sizes for different species, however in a comparison between species cottids tended to have larger and more variable gape widths with increasing body length than coastal cutthroat trout. When gape widths were compared to width of prey taxa, neither consumer appeared to be gape-limited. The smallest gape widths were for coastal cutthroat trout which were about 4 mm in width while the largest head width of any prey item



consumed during all months was only 4.1 mm. Overall prey taxa were small throughout all seasons.

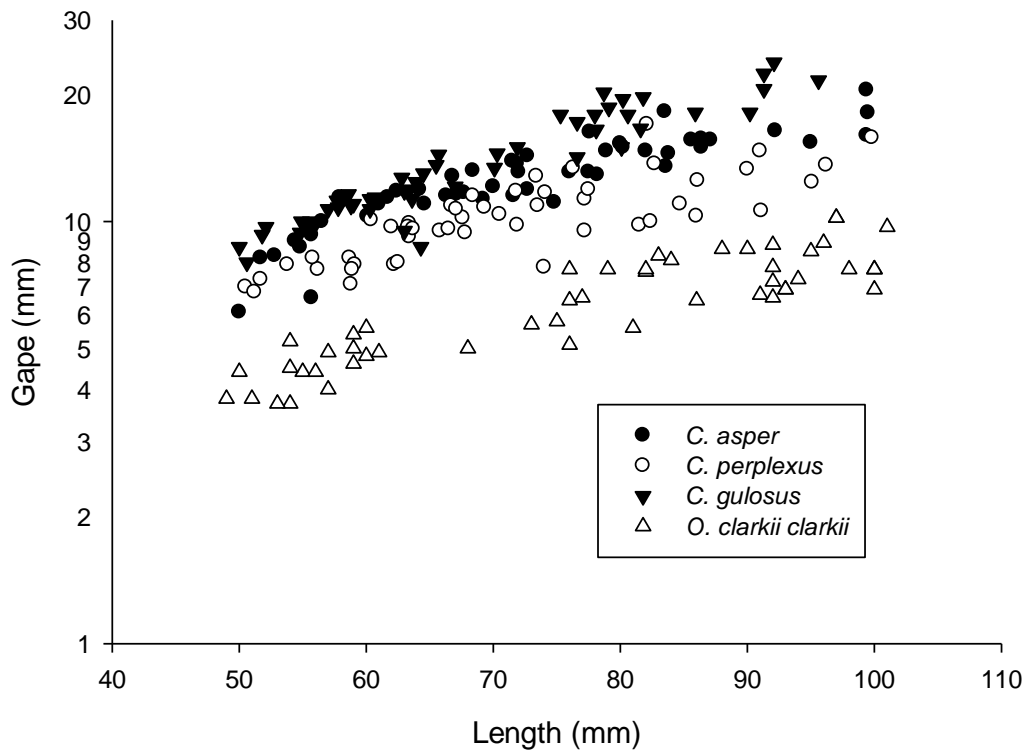


Figure 2.2. Log<sub>10</sub> transformed gape widths compared to length for prickly sculpin (*Cottus asper*), reticulate sculpin (*Cottus perplexus*), riffle sculpin (*Cottus gulosus*) and coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) from preserved specimens from Oregon State University's Fish Collection.

#### *Diet overlap*

Diet overlap based on Morisita's index (M) for aquatic macroinvertebrate prey counts were the lowest in May and peaked in September (Figure 2.3).

Among all comparisons levels of overlap considered to be biologically significant

( $M > 0.6$ ; Wallace 1981) were never observed. Diet overlap values between large coastal cutthroat trout and small coastal cutthroat trout was the lowest among all consumer comparisons in May ( $M=0.23$ ) and July ( $M=0.28$ ) yet had the highest overlap along with large coastal cutthroat and cottids in September ( $M=0.48$ ). Cottids and large coastal cutthroat maintained an intermediate level of diet overlap relative to May and July comparisons of other consumer classes. Diet overlap between cottids and small coastal cutthroat trout was the highest in May ( $M=0.32$ ) and July ( $M=0.48$ ) among all comparisons, but was the lowest among all comparisons in September ( $M=0.38$ ).

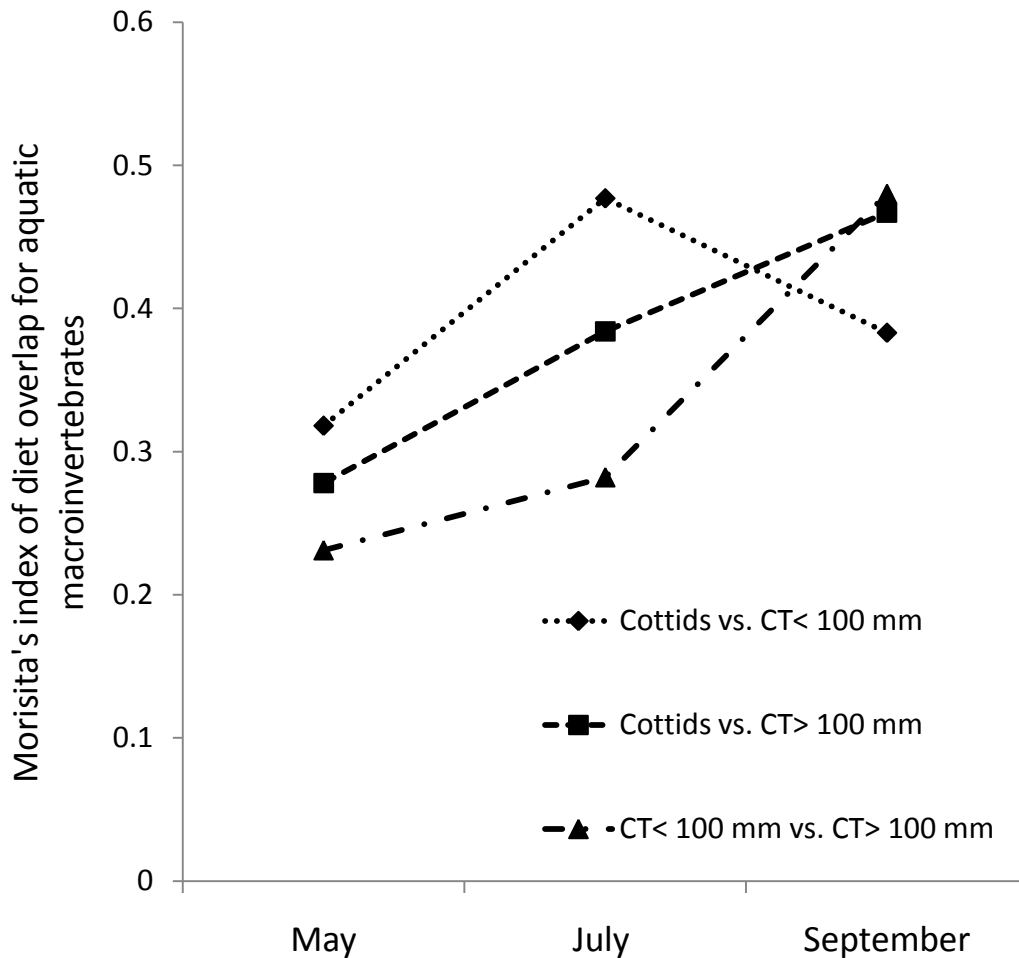


Figure 2.3. Seasonal comparisons of Morisita's index of diet overlap for aquatic macroinvertebrate prey of small coastal cutthroat trout (CT < 100 mm), large coastal cutthroat trout (CT > 100 mm) and cottids from stream sections in the Trask watershed during 2008 (Figure 2.1), based on prey counts (index is based on a scale of 0-1).

*Food limitation: direct observation*

Mean consumption rates of invertebrates (aquatic and terrestrial prey combined) were highest for all consumer classes in May (Figure 2.4). Differences in mean consumption rates between small coastal cutthroat trout, large coastal cutthroat trout and cottids were statistically different in May (Kruskal-Wallis test,

$X^2 = 8.25$ ,  $df = 2$ ,  $p < 0.01$ ). Cottids during May had lower mean consumption rates than coastal cutthroat trout. Additionally in July, mean consumption rates between small coastal cutthroat trout, large coastal cutthroat trout and cottids were different (Kruskal-Wallis test,  $X^2 = 16.31$ ,  $df = 2$ ,  $p < 0.01$ ). Again, cottids had the lowest mean consumption rates. Coastal cutthroat trout appeared to have higher consumption rates than cottids in September but these differences were not statistically significant, due to high variability in mean consumption rates within each consumer class. Differences in mean consumption rates among seasons for small cutthroat trout and large cutthroat were statistically significant (Kruskal-Wallis test,  $X^2 = 19.77$ ,  $df = 2$ ,  $p < 0.01$ ;  $X^2 = 20.68$ ,  $df = 2$ ,  $p < 0.01$ ).

Comparisons of prey types (aquatic versus terrestrial) consumed by coastal cutthroat trout and cottids revealed similarities for aquatic prey and differences for terrestrial prey. Mean aquatic macroinvertebrate consumption rates were highest in May for all consumer classes (Figure 2.5). Differences in mean aquatic macroinvertebrate consumption rates between small coastal cutthroat trout, large coastal cutthroat trout and cottids had only weak statistical differences in May (Kruskal-Wallis test,  $X^2 = 5.78$ ,  $df = 2$ ,  $p = 0.05$ ). Both size classes of coastal cutthroat trout had higher mean aquatic macroinvertebrate consumption rates than cottids. During July, small coastal cutthroat trout, large coastal cutthroat trout and cottids had weak statistical differences in aquatic

macroinvertebrate consumption rates (Kruskal-Wallis test,  $X^2 = 5.57$ ,  $df = 2$ ,  $p = 0.06$ ). Small and large coastal cutthroat trout again had higher consumption rates for aquatic macroinvertebrates than cottids. In September, consumption rates for aquatic macroinvertebrates were different between small coastal cutthroat trout, large coastal cutthroat trout and cottids (Kruskal-Wallis test,  $X^2 = 7.46$ ,  $df = 2$ ,  $p = 0.02$ ). However, absolute differences in the consumption rates for aquatic macroinvertebrates between consumer classes were small, yet large cutthroat trout had the highest aquatic macroinvertebrate consumption rates followed by cottids then small coastal cutthroat trout. Differences in the mean aquatic macroinvertebrate consumption rates among seasons for each consumer class—small coastal cutthroat trout, large coastal cutthroat trout and cottids were statistically significant (Kruskal-Wallis test,  $X^2 = 52.35$ ,  $df = 2$ ,  $p < 0.01$ ;  $X^2 = 41.73$ ,  $df = 2$ ,  $p < 0.01$ ;  $X^2 = 10.24$ ,  $df = 2$ ,  $p < 0.01$ ).

Smaller coastal cutthroat trout showed higher consumption rates of terrestrial invertebrates than large coastal cutthroat trout during May, July and September, although none of these differences were considered significant (Figure 2.6). Whereas differences among months for large and small cutthroat trout appeared to be similar as well, they too were not considered statistically significant. Consumption of terrestrial invertebrates by cottids was limited,

regardless of season. The maximum number of cottids consuming terrestrial invertebrates during any month was in July ( $n = 10$ ).

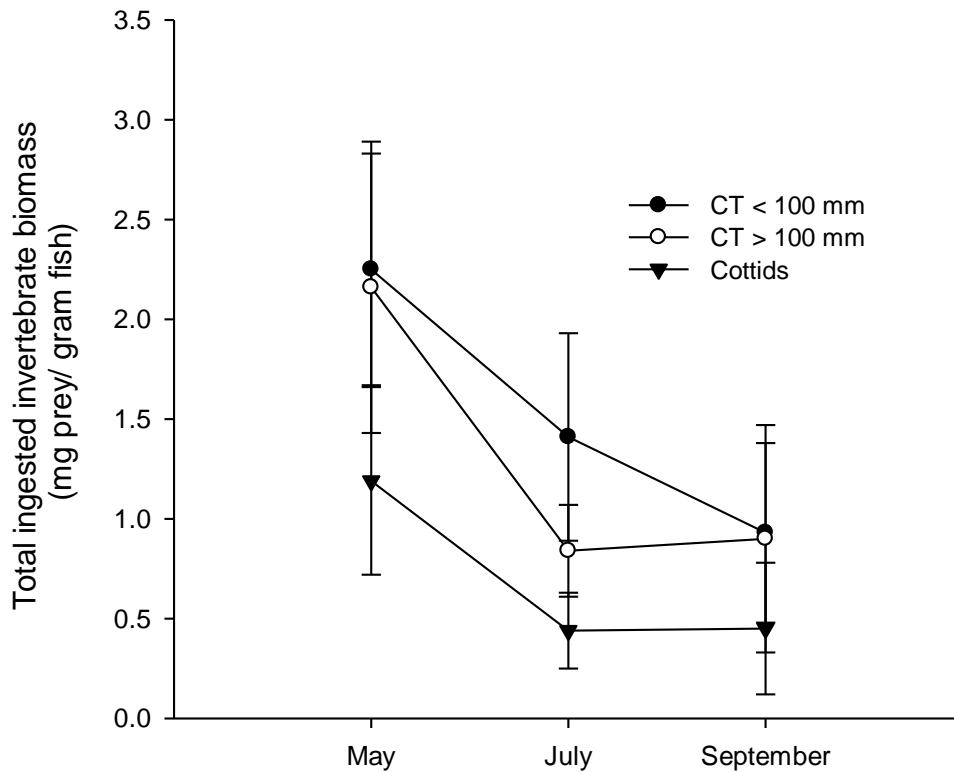


Figure 2.4. Seasonal changes of mean ingested invertebrate biomass (mg of prey/gram of fish) for small coastal cutthroat trout (CT < 100 mm), large coastal cutthroat trout (CT > 100 mm) and cottids from stream sections within the Trask watershed in 2008. Bars represent 95% confidence intervals.

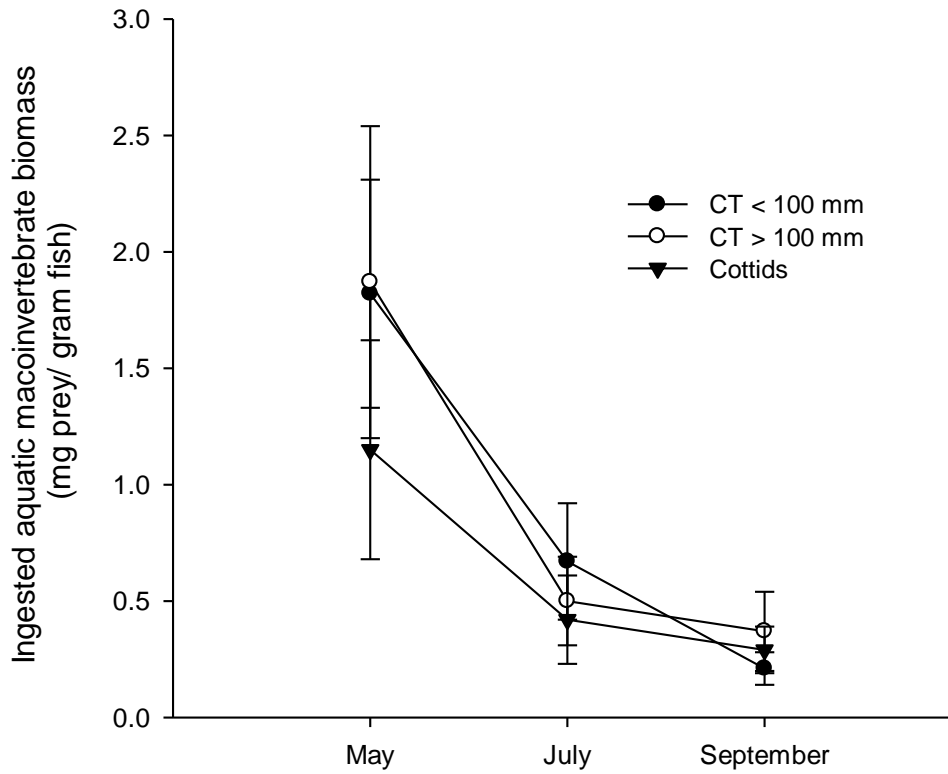


Figure 2.5. Seasonal changes of ingested aquatic macroinvertebrate biomass (mg of prey/gram of fish) for small coastal cutthroat trout (CT < 100 mm), large coastal cutthroat trout (CT > 100 mm) and cottids from stream sections within the Trask watershed in 2008. Bars represent 95% confidence intervals.

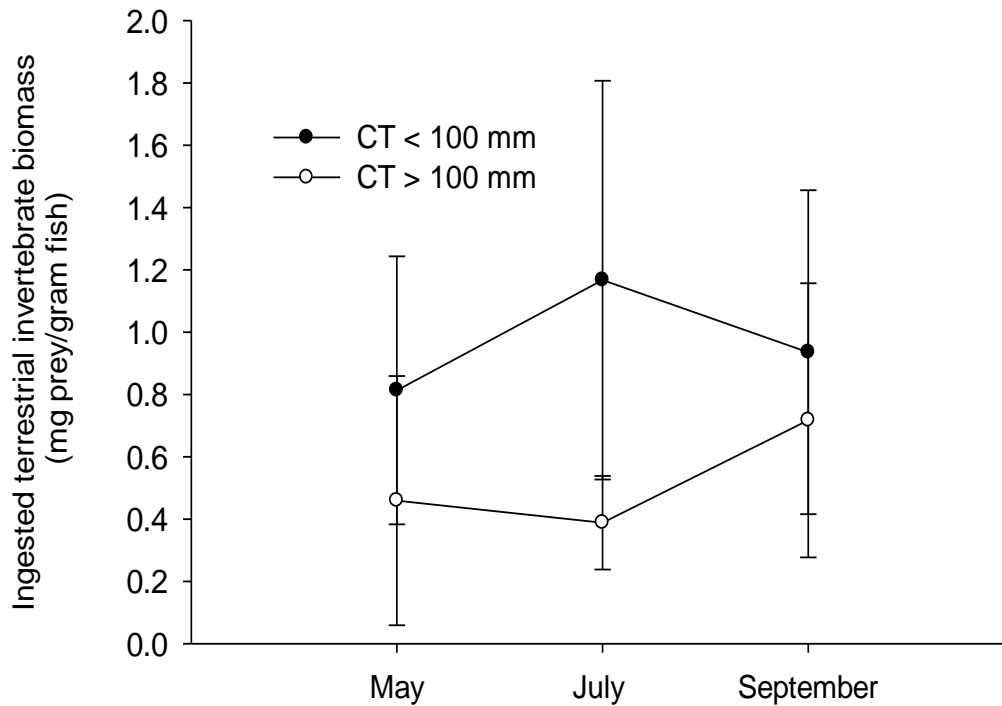


Figure 2.6. Seasonal changes in the mean ingested biomass of terrestrial invertebrates (mg of prey/gram of fish) for small coastal cutthroat trout (CT < 100 mm) and large coastal cutthroat trout (CT > 100 mm) from stream sections within the Trask watershed in 2008. Bars represent 95% confidence intervals.

Abundances of individual prey taxa consumed varied between seasons and among consumers (Figures 2.7-2.9). To compare diet richness between consumer classes at different abundances, I utilized taxa (family) accumulation curves to rarify the abundance of individual prey taxa to the lowest value between the two consumers being compared (Appendix C). In May, all consumer classes tended to have a similar pattern of diet richness (Figure 2.7), when Ephemeroptera represented a dominant proportion of the diet for each consumer class (Figure



2.10). During July (Figure 2.8) a clear disparity emerged between diet richness as both large and small coastal cutthroat trout have a richer diet compared to cottids. About half of the diets of cottids were represented by Ephemeroptera while half of the diet of large coastal cutthroat trout is composed of Ephemeroptera, Plecoptera, Trichoptera and Diptera and nearly half of the diet of small coastal cutthroat trout is composed of Ephemeroptera, Plecoptera and Trichoptera (Figure 2.11). Consumption of individual aquatic macroinvertebrates appeared to be lowest in September for all consumers (Figure 2.9). However, small cutthroat trout exhibited the most diverse diet within this month. Cottids relied on taxa from Ephemeroptera and Plecoptera to represent over half their diet within this month while coastal cutthroat trout consumed wide diversity of aquatic and terrestrial derived taxa (Figure 2.12). In summary, cottids exhibited a less diverse pattern of diet richness during July and September relative to coastal cutthroat trout (but were similar in May). Large and small coastal cutthroat trout had similar patterns of diet richness in May and July; in September, small coastal cutthroat trout exhibited a more diverse diet than large coastal cutthroat trout.

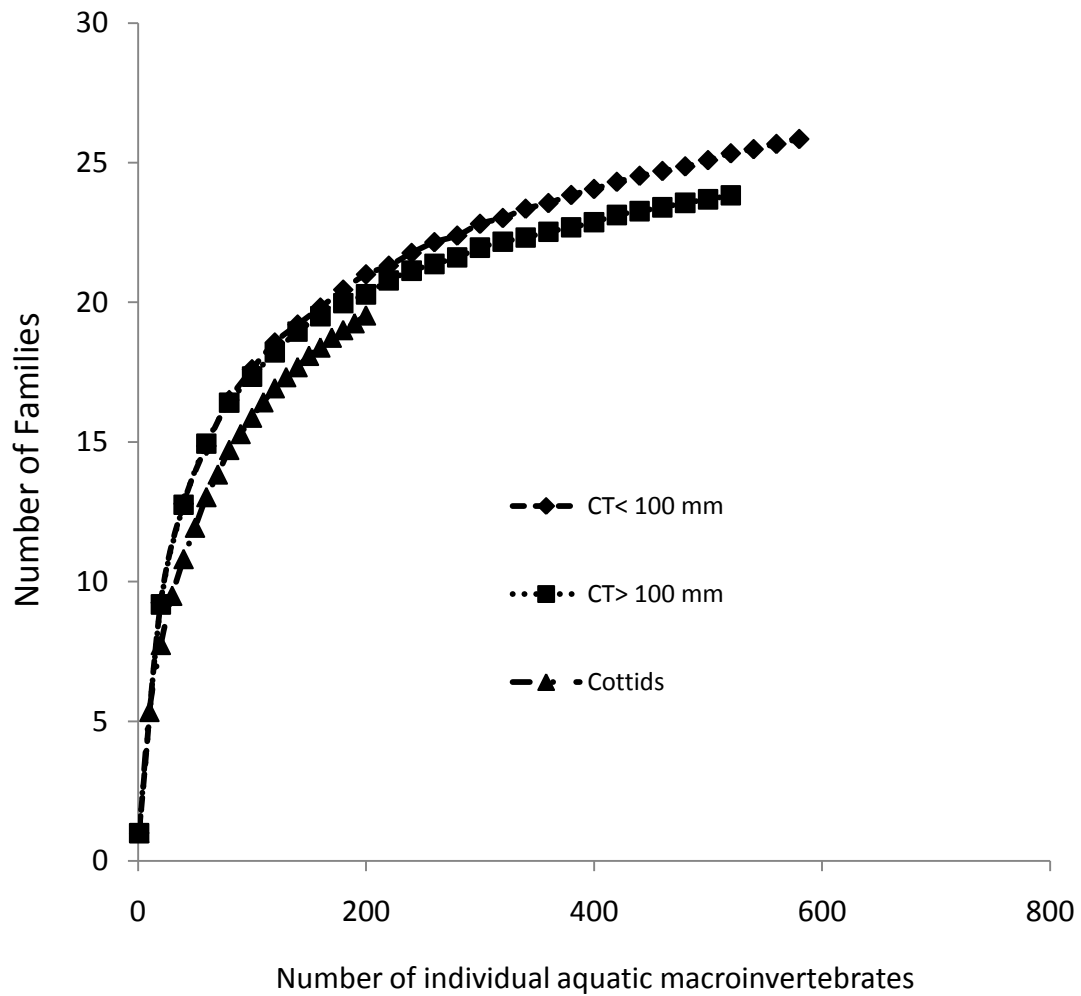


Figure 2.7. Family accumulation curve for the number of aquatic macroinvertebrates ingested by small coastal cutthroat trout (CT < 100 mm), large coastal cutthroat trout (CT > 100 mm) and cottids during May 2008 for stream sections within the Trask Watershed.

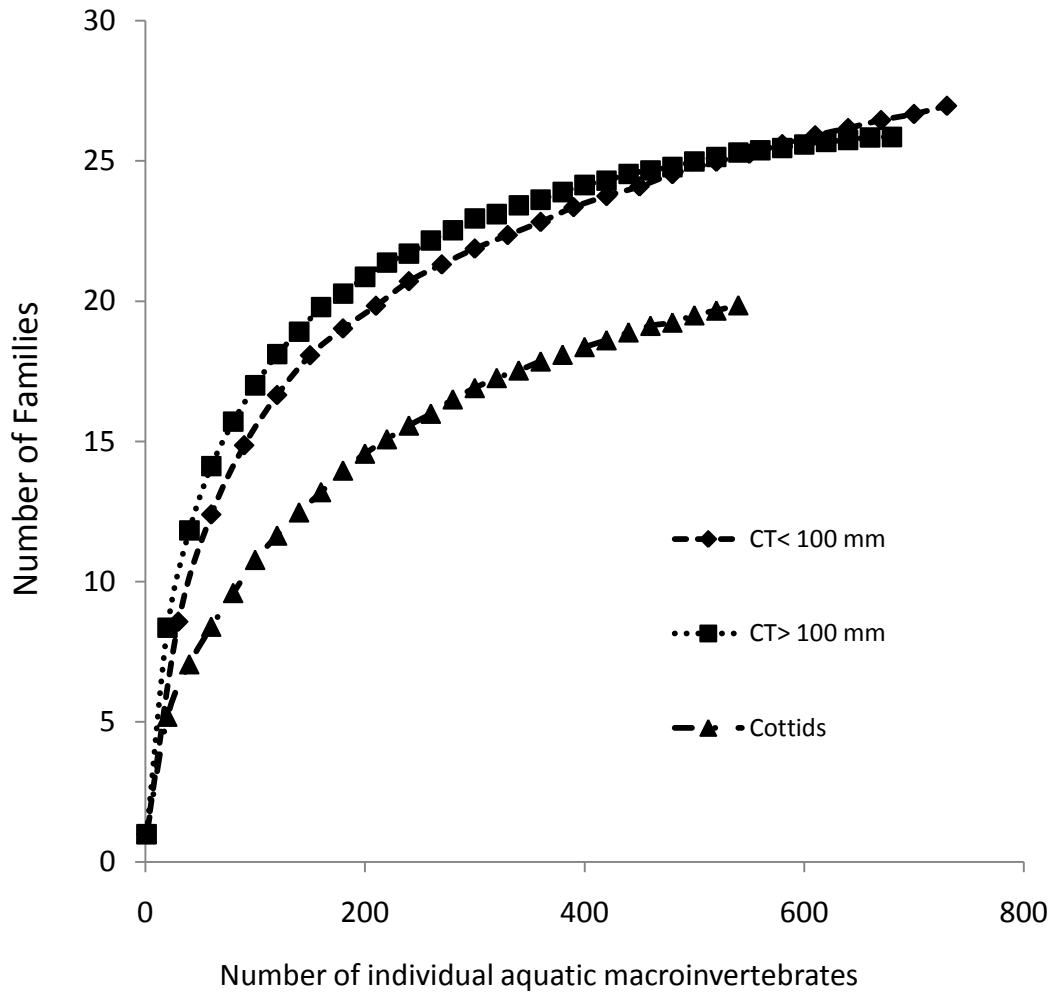


Figure 2.8. Family accumulation curve for the number of aquatic macroinvertebrates ingested by small coastal cutthroat trout (CT < 100 mm), large coastal cutthroat trout (CT > 100 mm) and cottids during July 2008 for stream sections within the Trask Watershed.

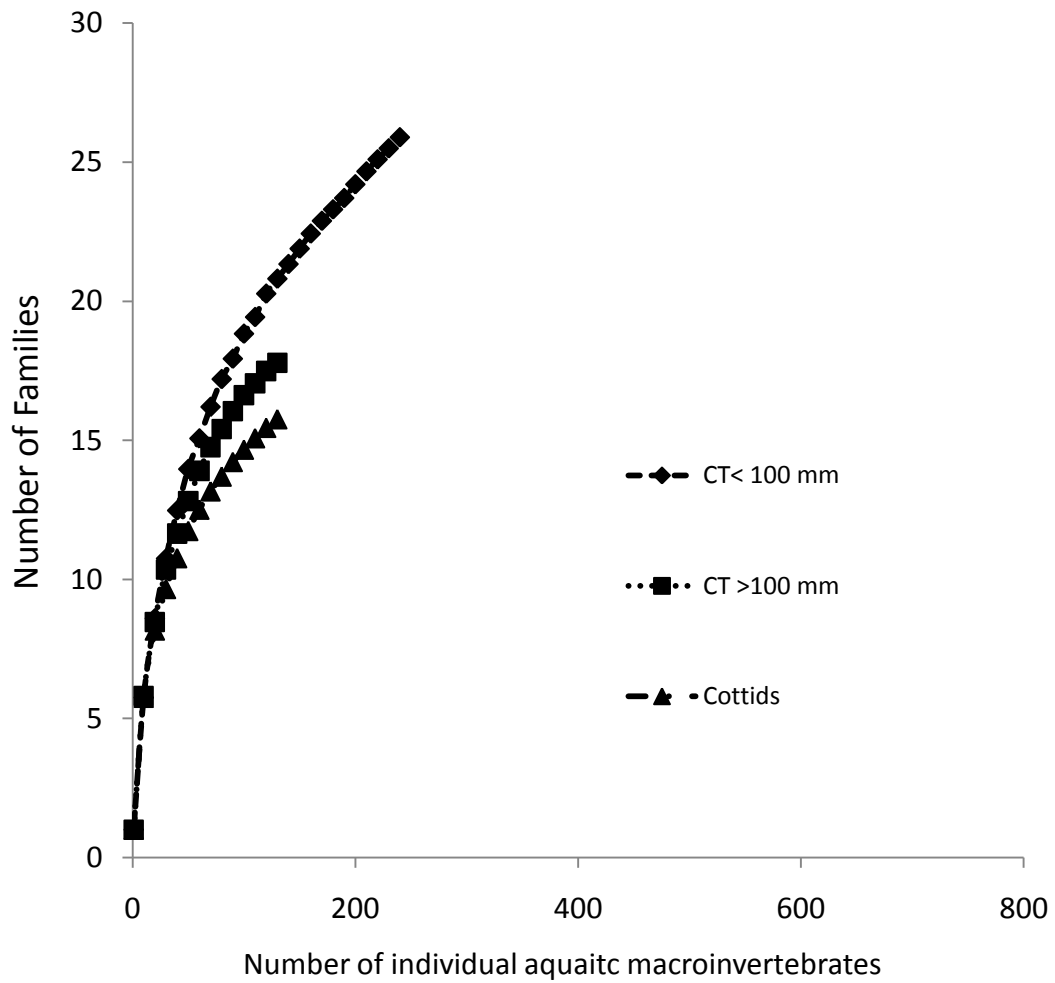


Figure 2.9. Family accumulation curve for the number of aquatic macroinvertebrates ingested by small coastal cutthroat trout (CT < 100 mm), large coastal cutthroat trout (CT > 100 mm) and cottids during September 2008 for stream sections within the Trask Watershed.

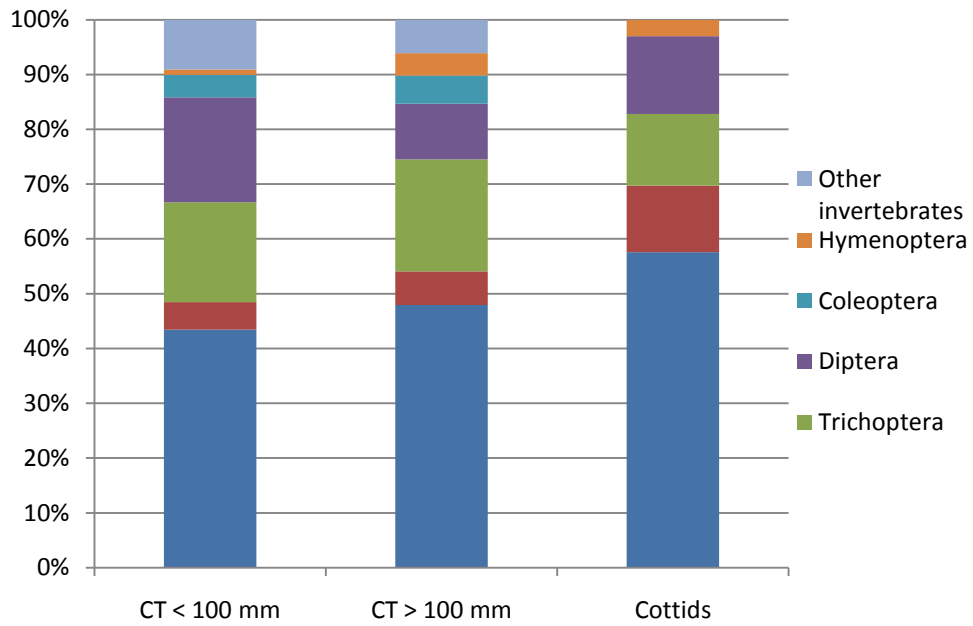


Figure 2.10. Mean diet proportions based on taxonomic order for small coastal cutthroat trout (CT < 100 mm), large coastal cutthroat trout (CT > 100 mm) and cottids during May 2008 from the Trask watershed.

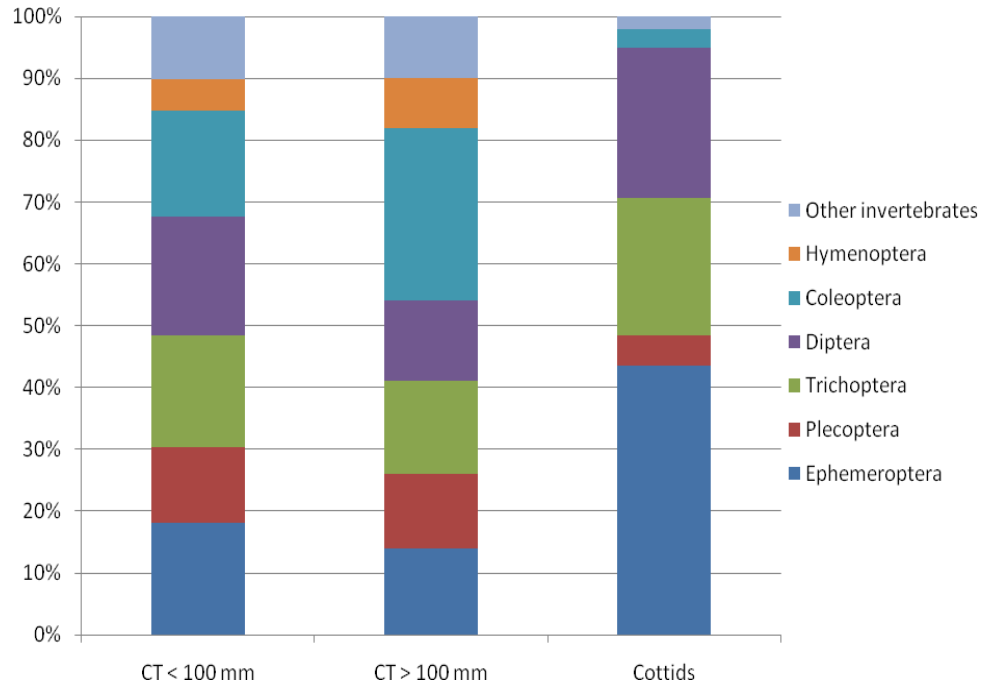


Figure 2.11. Mean diet proportions based on taxonomic order for small coastal cutthroat trout (CT < 100 mm), large coastal cutthroat trout (CT > 100 mm) and cottids during July 2008 from the Trask watershed.

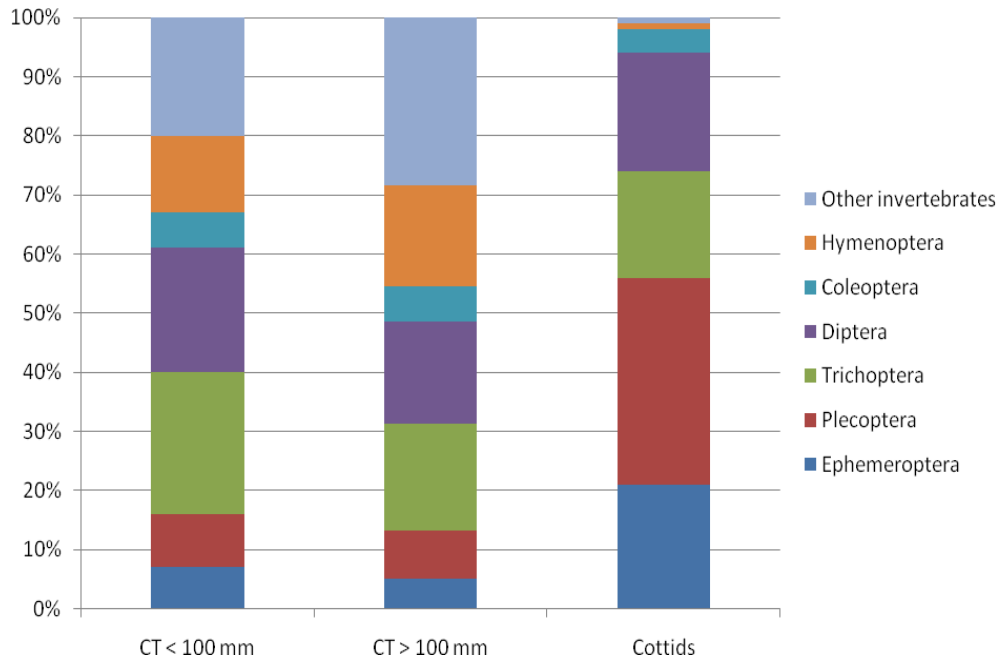


Figure 2.12. Mean diet proportions based on taxonomic order for small coastal cutthroat trout (CT < 100 mm), large coastal cutthroat trout (CT > 100 mm) and cottids during September 2008 from the Trask watershed.

*Food limitation: bioenergetics*

Estimates of consumption for individual large cutthroat trout from July to September ranged from 8% to 18% of maximum consumption ( $P$ -values), as estimated by the bioenergetics model. Modeled seasonal consumption for small cutthroat trout ranged from 8% to 16% of maximum consumption from July to September. Seasonal consumption for cottids varied from 29% to 54% of the maximum consumption. Differences in mean  $P$ -values between small coastal cutthroat trout, large coastal cutthroat trout and cottids were apparent (Kruskal-Wallis test,  $X^2 = 83.96$ ,  $df = 1$ ,  $p < 0.01$ ). Cottid mean  $P$ -values (0.38) were found to be nearly four times higher compared to small and large coastal cutthroat

trout (both 0.11). Growth data used to evaluate growth efficiency was low and similar for all consumer classes (Appendix D). Modeled mean growth efficiency tended to be similar between coastal cutthroat trout size classes and averaged only 1%, whereas mean growth efficiency of cottids was also low, but higher (4%; Table 2.4) in comparison to coastal cutthroat trout.

Table 2.4. Bioenergetics model output for small coastal cutthroat trout (CT < 100 mm), large coastal cutthroat trout (CT > 100 mm) and cottids from the Trask watershed in 2008. Numbers of individuals ( $n$ ) recaptured for growth measurements are indicated for each consumer class. Estimated consumption was derived from the Wisconsin Bioenergetics Model (Hanson et al. 1997). Growth efficiency (GE) was calculated by dividing the average growth from July to September by the model estimate of consumption ( $C$ ).  $P$  is the ratio of  $C$  to maximum consumption.

Consumer class	$n$	$C$ (g)	$P$	GE (%)
CT < 100 mm	113	14.16	0.11	1.00
CT > 100 mm	236	26.31	0.11	1.00
Cottids	31	7.58	0.38	4.00

### Discussion

Based on direct observation of nearly 340 individuals, it appeared that coastal cutthroat trout and cottids in systems studied herein relied primarily on invertebrate prey, with little evidence of intraguild predation (piscivory between species). Gape widths of coastal cutthroat trout and cottids suggested gape limitation to be unlikely due to the small size of prey relative to gape widths. Direct observation of diet composition suggested cottids were more food limited



than coastal cutthroat trout, particularly in July and September. Coastal cutthroat trout exhibited higher directly observed rates of prey consumed (based on mg prey/ gram of fish) of aquatic and terrestrial prey in May and July in addition to exhibiting a more diverse diet compared to cottids in July and September. These direct lines of evidence suggested cottids, not coastal cutthroat trout should be more food limited. When food limitation was viewed from a bioenergetic perspective which includes diet composition and energetic value as well as the physiology of the fish, the reverse appeared to be true: coastal cutthroat trout were more food limited during July and September. The different perspectives offered by direct observation and bioenergetic modeling of trophic relationships of coastal cutthroat trout and cottids provide several important insights into how these species respond to seasonal food limitation in headwater streams.

No fish in this study appeared to be gape-limited for macroinvertebrates due to the small size of prey consumed by all fish, regardless of gape width. Other studies in small streams support our findings that the use of similar, small size prey among different size classes is common and gape-limitation is unlikely in small streams (Allan 1981; Bozek et. al 1994). Whereas intraguild predation was not documented during this study other studies have identified the importance of intraguild predation between native species (Browne and Rasmussen 2009) and

between native and introduced species (Taniguchi et. al 2002) that either induced habitat shifts or increased recruitment for the introduced species (latter).

Overall patterns of predation by coastal cutthroat trout and cottids could be interpreted to suggest that cottids may be more food limited from July to September because they consumed a lower diversity of prey and in lower quantities. In contrast to these observations, bioenergetic modeling suggested that coastal cutthroat trout were more food limited than cottids, at least between July and September. Although coastal cutthroat trout had higher total mean consumption rates within this timeframe than cottids, little growth was accrued for either species. This suggests coastal cutthroat were not able to meet their basic metabolic needs during this time period. Before growth can be achieved, energy from consumed prey must be directed towards maintaining basic metabolic processes and processes associated with egestion and excretion. Whereas energetic costs associated with egestion and excretion are typically assumed to be low (Hanson et al. 1997), they may be important in some cases (Bajer et. al 2004). Activity costs, which were not explicitly modeled here, may also be important (Boisclair and Leggett 1989; Hartman and Hayward 2007). Differences in behavior and morphology of cottids and coastal cutthroat trout suggest the latter may experience higher activity costs.

The benthic nature of cottids may be the most obvious difference resulting in lower activity costs relative to coastal cutthroat trout. Because of their lack of a swim bladder, relatively large pectoral fins and their dorsoventrally flattened body morphology, cottids should be able to efficiently maneuver within the benthos, while avoiding the energetic costs that salmonids experience by actively swimming within the water column (at higher velocities) potentially interacting with other conspecifics to maintain or acquire profitable foraging positions (Fausch 1984).

Another important difference between coastal cutthroat trout and cottids may relate to how each responds to the threat of terrestrial predators (e.g., birds and mammals; Steinmetz et. al 2003) during seasonal low flows. Predation by terrestrial predators has been suggested as a reason for why decreased survival of coastal cutthroat trout is lowest during late summer and early fall low flows (Berger and Gresswell 2009). To avoid predation by terrestrial predators, coastal cutthroat trout rely on active evasion or concealment (Allouche 2002). In small streams, concealment may be particularly important; as instream cover is very limited for coastal cutthroat trout in streams I studied (Andersen 2008). That may result in increased energy costs searching for cover or chronically evading predators if sufficient cover is not detected. Smaller conspecifics may also be forced into shallower habitats near stream margins by larger fish to avoid in-

stream predators (Moore and Gregory 1988) but may also be more subject to terrestrial predation as a result. In contrast to coastal cutthroat trout, cottids can presumably avoid detection by terrestrial predators through their small body size, cryptic coloration and through a tendency for more nocturnal activity (Patten 1971). Accordingly, activity associated with predator avoidance (cover and evasion) may be more important for coastal cutthroat trout than cottids during seasonal low flows and may result in higher energetic expenditure.

Differences in the metabolic costs associated with digestibility of prey among coastal cutthroat trout and cottids may also explain bioenergetic differences in July and September. During this time period, terrestrially derived prey become increasingly important for coastal cutthroat trout, whereas cottids continue to rely almost exclusively on aquatic prey and these prey types may differ in terms of their digestibility (due to sclerites, secondary defense compounds, etc; Hess and Rainwater 1939, Hyslop 1980). Thus, terrestrial prey may be larger and more energy-dense overall (McCarthy et. al. 2009), but less digestible to consumers. There may have also been unaccounted sources of error related to conversions of dry weight to wet weight associated with retention rates of prey, sampling errors, estimates of energetic content and digestibility rates of prey. For example, if cottids consumed prey with greater digestibility in

comparison to coastal cutthroat trout, then the assimilation efficiency of the latter would be reduced, explaining the difference in relative  $P$ -values observed.

In summary, I could only speculate on the processes that accounted for differences in the performance of coastal cutthroat trout or cottids during low-flow periods. The important point is that direct observation and bioenergetic models lead to different potential interpretations of food limitation in terms of comparing coastal cutthroat trout to cottids. Two processes, activity costs and digestibility of prey, seem to be plausible explanations for differences among consumers in food limitation. Future study focusing more on these factors could help to better understand why these species appear to be so different.

#### *Implications for species interactions*

Given that cottids and cutthroat trout have co-existed for millennia in Pacific Northwest headwater streams, they may partition resources along one or many niche axes (Connell 1980). Differences in diet composition and consumption rates may simply be a function of different foraging opportunities as a result of being a benthic (cottids) and water column dwelling fish (salmonids). Resource partitioning may not be limited to prey only, as evidence in small streams has shown larger salmonids select deeper habitat with higher velocities in order to decrease predation risk and increase survival (Railsback and Harvey 2002). Even though salmonids may select deeper habitats, other studies have

revealed strong vertical segregation within the water column between benthic fish and salmonids (Baltz and Moyle 1984). Another axis of potential divergence between the two species may be related to diel activity. Cottids are suspected to be nocturnally active compared to salmonids, which exhibit multiple and complex diel activity patterns (Reebs 2002). Studies during the summer have found that most often, salmonids feed during the day and seek cover at night (Young et. al 1997; Bradford and Higgins 2001). Regardless, given the multitude of ways in which cottids and coastal cutthroat trout may partition resources within headwater streams, opportunities for interspecific competition may be limited in nature.

Although my results suggested limited potential for interspecific competition between cottids and salmonids in the streams I studied, experimental studies in other systems have indicated it can be an important process. For example, in an experimental stream channel with sympatric Siberian sculpin *Cottus poecilopus*, brown trout occupied a higher proportion of finer substrates than in allopatry while Siberian sculpin occupied the larger preferred substrates, suggesting interference competition (Hesthagen and Heggenes 2003). Another study using stream enclosure experiments found growth of large cottids to be reduced in the presence of brown trout, but not in the presence of native brook trout even though differences in the diet composition were not detected (Zimmerman and Vondracek 2007). Studies of species interactions by use of

experiments are helpful because they allow investigators to control species densities and potentially reveal important variables influencing intraspecific or interspecific competition (Connell 1983). However inferences made using experimental treatments may be biased, because the treatment design may force competition to occur or introduce artifacts and situations unlikely to occur under natural settings (Gelwick and Matthews 1993). Furthermore the results can be difficult to relate to field conditions because experimental treatments designed to examine competition often fail to appropriately account for species composition and overall density among treatments (Inouye 2001). Whereas the strength of interspecific competitive interactions cannot be reliably inferred from patterns of resource use alone (Crowder 1990), evidence for food limitation during low flows highlights the potential role of intraspecific competition, which should be more likely (Ward et. al 2006).

#### *Intraspecific interactions*

Because coastal cutthroat trout may be more food limited than cottids, intraspecific competition may be more intense among conspecifics interacting for prey critical to survival during peak periods of resource scarcity. When food limiting conditions persist over prolonged periods within streams, growth decreases as the probability of mortality via starvation increases (Railsback et. al 1999). As a result, risk taking behaviors may increase as the associated tradeoffs of starving versus predation risk begin to tilt towards avoiding starvation to

increase growth at the risk of being potentially subject to predation (Railsback et. al 1999; Dill and Fraser 1984). Fish may exhibit habitat or behavioral shifts in the presence of predators at the cost of maintaining a lower foraging rate (Gilliam and Fraser 1987). Subsequently, reduced rates of foraging may lead to emigration in salmonid fishes (Keeley 2001; McMahon and Matter 2006). Besides emigration localized abundances of fish may also decline as a result of mortality via predation.

In contrast to potentially strong intraspecific competition among coastal cutthroat trout resulting in decreased abundances, intraspecific competition may not be as intense among cottids, at least with respect to the sizes of individuals studied herein. It is quite possible that smaller (<55 mm, SL) cottids may experience adverse impacts from intraspecific competition with larger individuals, as demonstrated in long-term research on *C. bairdi* in another system (Grossman et al. 2006). Regardless, cottids occurred at higher densities and were less food limited within the Trask watershed compared to coastal cutthroat trout suggesting the impact of intraspecific competition may be less pronounced in terms of individuals or populations.

### *Conclusion*

In conclusion, the use of a bioenergetics model was a vital tool in revealing the importance of incorporating physiology along with diet for



comparing species from different taxonomic orders. Diet information used in concert with a bioenergetic model suggested a greater portion of the energy budget of coastal cutthroat was devoted towards maintaining basic metabolic processes, related to finding cover, foraging, predator avoidance or digestion. Future studies should seek to explicitly examine how these activities or other costs influence the energetic budget of cottids and coastal cutthroat trout. Additional study of how cottids and coastal cutthroat trout may partition resources based on their behavior and morphological characteristics would also prove useful for understanding species interactions and autecologies. While the role of interspecific competition cannot be ruled out, intraspecific competition may be more severe for coastal cutthroat trout than cottids and is perhaps related to decreased abundances of coastal cutthroat trout, whereas densities of cottids tends to be higher. Furthermore, the relative impacts upon aquatic food webs by consumers other than salmonids, including salamanders (Zardiac 2003) and cottids may be greater than currently acknowledged due to their potential to outnumber salmonids in abundance or biomass (Hawkins et. 1983). The importance of these consumers may vary seasonally, as well as the consequences for individuals, population processes, and ecosystem impacts (e.g. Power et al. 2008).

### CHAPTER 3- GENERAL CONCLUSIONS

Results of this study suggest incorporating physiological information in concert with diet composition is an important and often overlooked aspect when interpreting predation patterns. Based on diet composition alone, cottids appear to be more food limited than coastal cutthroat trout. Coastal cutthroat trout exhibited a more diverse diet in addition to having higher aquatic and terrestrial rates of consumption than cottids during July and September. However including the physiology of the fish with diet composition as well, reveals coastal cutthroat trout are more food limited than cottids during the July to September period. The associated costs related to searching for cover, foraging, temperature and predator avoidance result in greater energy demands to maintain basic metabolic processes compared to cottids. Furthermore, future studies should seek to explicitly examine how activities associated with finding cover, foraging, avoiding predators and temperature directly relate to the energetic budget of cottids and coastal cutthroat trout to further current knowledge about how these factors effect food limitation experienced by cottids and coastal cutthroat trout.

Cottids and coastal cutthroat trout appear unlikely to interact for prey taxa based on their diet composition and the multiple ways in which they may partition resources. Whereas the role of interspecific competition cannot be ruled out, but intraspecific competition may be more severe for coastal cutthroat trout than cottids because they appear to be more food limited, resulting in a greater

propensity to take part in risk taking behaviors potentially resulting in lower abundances due to emigration or mortality relative to cottids within headwater streams.

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**APPENDICES**

Appendix A—Redundancy of bioenergetic model output

Table A-1. Pearson correlation tables between bioenergetic parameters to evaluate redundancy of output for each consumer class.

CT > 100 mm	<i>P</i> -value	Consumption	GE
<i>P</i> -value	1		
Consumption	0.72	1	
GE	0.86	0.35	1

CT < 100 mm	<i>P</i> -value	Consumption	GE
<i>P</i> -value	1		
Consumption	0.79	1	
GE	0.93	0.65	1

Cottids	<i>P</i> -value	Consumption	GE
<i>P</i> -value	1		
Consumption	0.77	1	
GE	0.81	0.32	1

Appendix B—Raw diet data

Table B-1. Number of stomach samples collected by consumer class, month and site.

Consumer class	Month	Site	Number of stomachs
CT < 100 mm	May	Pothole	11
CT < 100 mm	May	Rock	11
CT < 100 mm	May	Gus	8
CT < 100 mm	May	UPM	12
CT > 100 mm	May	Pothole	3
CT > 100 mm	May	Rock	6
CT > 100 mm	May	Gus	5
CT > 100 mm	May	UPM	9
Cottids	May	Pothole	6
Cottids	May	Rock	14
Cottids	May	Gus	0
Cottids	May	UPM	7
CT < 100 mm	July	Pothole	9
CT < 100 mm	July	Rock	9
CT < 100 mm	July	Gus	10
CT < 100 mm	July	UPM	10
CT > 100 mm	July	Pothole	9
CT > 100 mm	July	Rock	10
CT > 100 mm	July	Gus	11
CT > 100 mm	July	UPM	9
Cottids	July	Pothole	10
Cottids	July	Rock	18
Cottids	July	Gus	10
Cottids	July	UPM	10
CT < 100 mm	September	Pothole	10
CT < 100 mm	September	Rock	10
CT < 100 mm	September	Gus	9
CT < 100 mm	September	UPM	10
CT > 100 mm	September	Pothole	8
CT > 100 mm	September	Rock	10
CT > 100 mm	September	Gus	9
CT > 100 mm	September	UPM	9
Cottids	September	Pothole	9
Cottids	September	Rock	8
Cottids	September	Gus	6
Cottids	September	UPM	10

Table B-2. Raw diet data collected from May 20 to September 19, 2008 with the calculated biomass estimates of soft larvae (SL), rigid larvae (RL), aquatic nymphs (AN), aquatic adults (AA), other terrestrial (OT), coleopteran adults (CA) and hymenoptera (HY) consumed sorted by date, site and species.

Fish ID	Date	Site	Species	Length (mm)	Weight (g)	SL (mg)	RL (mg)	AN (mg)	AA (mg)	OT (mg)	CA (mg)	HY (mg)
1A05	5/22/2008	T1	CT	80	6.7	0.17	0.57	1.73	0	0	0	0
1A08	5/22/2008	T1	CT	84	7.8	0.17	1.3	0	0	7.17	0	0
1A11	5/22/2008	T1	CT	78	6	0.73	3.71	1.18	0	0	0	0
1A15	5/22/2008	T1	CT	83	7.8	2.53	1.45	0	0	0	0.04	0
1A36	5/21/2008	T1	CT	76	5.2	0.19	7.23	9.65	0	1.48	0	0
1A37	5/21/2008	T1	CT	76	5.2	2.25	0	4.41	0	1.36	0	0
1A42	5/21/2008	T1	CT	98	11.6	1.56	18.73	6.24	0	0.78	0	11.7
1A43	5/21/2008	T1	CT	104	13.7	2.01	2.3	23.83	0.29	0.29	0	0
1A44	5/21/2008	T1	CT	74	5.4	0.25	0	0	0	0	0	0
1A47	5/21/2008	T1	CT	99	10.5	0	6.98	2.72	0	0	0	0
1A48	5/21/2008	T1	CT	117	21.7	19.2	1.35	6.06	0	0	7.07	0
1A49	5/21/2008	T1	CT	98	10.6	1.88	1.25	17.74	0	0	0	0
1A81	5/21/2008	T1	CT	78	5.8	3.17	3.06	3.39	0	0.22	1.09	0
1A94	5/22/2008	T1	CT	114	20.3	4.18	9.88	4.94	0	0	0	0
1A16	5/21/2008	T5	CT	81	7.3	0	1.34	13.66	0	11.78	0	0
1A19	5/22/2008	T5	CT	75	5.1	1.04	0	6.4	0	0	0	0
1A21	5/21/2008	T5	CT	94	9.6	0.62	1.08	13.77	0	0	0	0
1A24	5/21/2008	T5	CT	85	8.6	7.98	2.47	6.46	0	1.9	0.19	0
1A26	5/21/2008	T5	CT	154	41.3	0	15.25	15.25	0	6.1	0	14.23



1A33	5/20/2008	T5	CT	106	15.7	0.13	0.13	9.85	0	0.78	2.07	0
1A40	5/21/2008	T5	CT	96	10.5	0.35	6.62	27.88	0	0	0	0
1A46	5/21/2008	T5	CT	80	7	0	0	5.65	0.78	1.75	11.29	0
1A52	5/21/2008	T5	CT	144	38.9	26.96	11.8	57.3	5.06	60.67	6.74	0
1A78	5/21/2008	T5	CT	125	24.7	15.33	12.04	15.33	0	4.38	5.48	56.94
1A82	5/21/2008	T5	CT	98	10.8	6.62	0	6.75	0	0.14	0	0
1A83	5/21/2008	T5	CT	92	9.9	0	4.64	2.32	0	3.21	7.68	0
1A84	5/21/2008	T5	CT	101	14.5	0	0	2.82	0	0	0	0
1A88	5/21/2008	T5	CT	91	8.6	0.81	1.42	15.26	1.22	1.63	0	0
1A89	5/21/2008	T5	CT	84	7.7	0	9.34	3.45	0	0	0	0
1A91	5/21/2008	T5	CT	99	12	0.66	2.62	6.78	1.09	2.62	8.09	0
1A92	5/21/2008	T5	CT	110	16.7	0.91	3.05	21.92	1.22	3.35	0	0
1A06	5/22/2008	T8	CT	76	4.9	0.21	0	0	0	0	0	0
1A07	5/22/2008	T8	CT	155	37	2.6	26.03	58.12	0	0	0	0
1A10	5/22/2008	T8	CT	76	7.4	3.5	0	9.09	0	25.51	0	0
1A12	5/22/2008	T8	CT	69	4.1	0.16	0	0.98	0	0	0	0
1A01	5/22/2008	T8	CT	98	14	7.91	22.14	37.97	0	0	0	11.07
1A02	5/22/2008	T8	CT	88	7.3	0.71	0	11.13	0	0	0	0
1A03	5/22/2008	T8	CT	127	23.1	18.99	37.98	65.83	0	3.8	0	0
1A22	5/22/2008	T8	CT	110	18	2.82	19.05	45.87	0	2.82	0	0
1A90	5/22/2008	T8	CT	82	7.6	0.37	0	6.97	0	0	0	0
1A93	5/22/2008	T8	CT	113	18.9	27.82	54.53	22.26	6.68	0	0	0
1A96	5/22/2008	T8	CT	96	12.2	27.68	59.06	5.54	0	0	0	0
1A97	5/22/2008	T8	CT	100	12.8	3.93	21.69	10.37	0	0.36	0	0
1A04	5/22/2008	T8	CT	124	22.4	12.01	0	17.29	0	0	0	0

1A28	5/20/2008	UPM	CT	92	9.9	0	0	7.28	0	0	0	0
1A29	5/20/2008	UPM	CT	93	9	21.59	5.4	28.34	0	0	0	12.15
1A30	5/20/2008	UPM	CT	92	10.4	1.51	15.45	6.4	0	14.32	0	0
1A31	5/20/2008	UPM	CT	88	7.2	18.11	2.79	9.05	0	4.87	0	0
1A38	5/20/2008	UPM	CT	134	30.4	0	8.26	5.26	0	3.19	2.06	0
1A45	5/21/2008	UPM	CT	107	16.3	18.13	9.89	49.44	0	4.94	0	0
1A53	5/20/2008	UPM	CT	60	2.7	0.1	0	0.54	0	0	0	0
1A54	5/20/2008	UPM	CT	118	19.8	0.33	11.05	8.04	0	9.71	4.35	0
1A55	5/20/2008	UPM	CT	95	9.3	0.13	2.37	2.37	0	7.25	1.05	0
1A56	5/20/2008	UPM	CT	122	24.8	0	10.79	13.24	0.49	0	0	0
1A58	5/20/2008	UPM	CT	119	20	0.1	0.1	3.46	0.63	6.19	0	0
1A59	5/20/2008	UPM	CT	102	13	0	5.8	9.44	0.66	0.66	0	0
1A64	5/20/2008	UPM	CT	146	32.2	1.5	1.92	15.61	2.35	0	0	0
1A65	5/20/2008	UPM	CT	64	2.8	0.11	0	0	0.42	0	0	0
1A66	5/20/2008	UPM	CT	98	10	1.69	12.09	4.84	0	4.59	0.97	0
1A67	5/20/2008	UPM	CT	86	7.3	0.31	0	14.98	0	0	0	0
1A68	5/20/2008	UPM	CT	74	4.4	0.07	0.07	3.49	0	0	0	0
1A69	5/20/2008	UPM	CT	75	5.5	0.31	0.13	1.12	0.09	0.16	0	0
1A71	5/20/2008	UPM	CT	91	8.9	0.48	4.32	12.97	0.48	29.77	0	0
1A72	5/20/2008	UPM	CT	92	9.4	4.29	4.29	16.15	0.5	0	0	0
1A73	5/20/2008	UPM	CT	129	25.2	0.82	0	10.58	0.35	0	0	0
1A74	5/20/2008	UPM	CT	114	18.6	3.76	0.25	11.56	2.51	0	7.03	0
1A14	5/22/2008	T1	SC	56	3.6	0.19	0	0	0	0	0	0
1A32	5/21/2008	T1	SC	62	4.9	0.09	4.6	4	0	0	0	0
1A35	5/21/2008	T1	SC	56	3.6	0.04	0	0.59	0	0	0	3.31

1A41	5/21/2008	T1	SC	57	3.6	0.1	4.39	0.67	0	0	0	0
1A50	5/21/2008	T1	SC	65	6.1	0.5	0	0.25	0	0	0	0
1A51	5/21/2008	T1	SC	58	12.1	0.05	0.24	0	0	0	0	0
1A13	5/21/2008	T5	SC	96	20.9	0	0	134.84	0	0	0	0
1A17	5/21/2008	T5	SC	69	8.6	0.78	0	0.7	0	0	0	0
1A18	5/21/2008	T5	SC	68	7.7	0	3.6	23	0	1.11	0	0
1A20	5/21/2008	T5	SC	54	4.3	0.46	0	14.78	0	0	0	0
1A23	5/21/2008	T5	SC	72	9.8	0	0	29.63	0	0	0	0
1A25	5/21/2008	T5	SC	55	4.2	0	7.18	7.18	0	0	0	0
1A75	5/21/2008	T5	SC	66	7.8	0	0	0.39	0	0	0	0
1A76	5/21/2008	T5	SC	66	6.5	0	0.11	11.35	0	0	0	0
1A77	5/21/2008	T5	SC	68	7.6	0	0	5.8	0	0	0	0
1A79	5/21/2008	T5	SC	81	11.5	12.04	0.2	8.16	0	0	0	0
1A80	5/21/2008	T5	SC	80	10.2	0.17	2.25	14.87	0	0	0	0
1A85	5/21/2008	T5	SC	61	4.3	0	0	1.07	0	0	0	0
1A86	5/21/2008	T5	SC	90	17.2	8.69	1.39	7.3	0	0	0	0
1A95	5/21/2008	T5	SC	76	10.2	0.053	0	2.57	0	0.027	0	0
1A27	5/20/2008	UPM	SC	60	4.8	0.25	0	8	0	0	0	0
1A39	5/20/2008	UPM	SC	69	6.9	0.11	1.17	9.33	0	0	0	0
1A57	5/20/2008	UPM	SC	60	5	0	0.15	2.39	0	0	0	0
1A60	5/20/2008	UPM	SC	65	5.8	0.11	0	0.53	0	0	0	0
1A61	5/20/2008	UPM	SC	65	6	0	0	1.11	0	0	0	0
1A62	5/20/2008	UPM	SC	64	5.3	0	0	1.44	0	0	0	0
1A63	5/20/2008	UPM	SC	57	4.2	0.03	0	2.87	0	0	0	0
1B99	7/26/2008	T1	CT	95	10.8	0.04	1.39	0.29	0	0.24	0	0

1B100	7/26/2008	T1	CT	106	12	1.36	0.7	0.12	0.15	0.7	0	0
1B104	7/26/2008	T1	CT	95	9.4	0	2.71	1.8	0.23	17.81	0	0
1B105	7/28/2008	T1	CT	103	14.3	0.06	0.19	0.2	0	0.18	0	0
1B110	7/26/2008	T1	CT	112	16.4	13.11	0	0.42	0	5.92	0	1.69
1B112	7/26/2008	T1	CT	106	12.8	0.66	0	3.58	0	3.07	0	0
1B114	7/26/2008	T1	CT	121	17	0.36	0	3.24	1.98	5.21	0	7.19
1B118	7/26/2008	T1	CT	107	17	0.1	0	0.04	0	0	0	0
1B120	7/26/2008	T1	CT	94	8.8	0	0	0.36	0	0	35.87	0
1B121	7/26/2008	T1	CT	98	10.3	0.5	1.51	0.5	0.25	4.54	15.88	2.02
1B138	7/26/2008	T1	CT	96	10.9	0	0	0.21	0	0	0	0
1B141	7/26/2008	T1	CT	91	10.3	0.68	0.68	5.18	0	16	0	0
1B142	7/26/2008	T1	CT	120	22.4	0.26	3.12	0	0	2.6	20.03	0
1B146	7/26/2008	T1	CT	108	13.2	0.26	1.28	2.82	0.26	2.05	18.2	0.77
1B148	7/26/2008	T1	CT	116	19.2	30.38	0.32	1.28	0	0	0	0
1B149	7/26/2008	T1	CT	87	8.2	1.16	0.48	1.1	3.26	0.82	0	0
1B185	7/27/2008	T1	CT	94	9.2	0.23	2.49	0.06	0.12	0	0	0
1B209	7/26/2008	T1	CT	94	8.7	0	0	0.1	9.63	0.1	0	0
1B152	7/27/2008	T5	CT	88	7.7	7.39	0.12	0	0	2.09	0	2.71
1B154	7/27/2008	T5	CT	132	29	0	2	4.01	14.03	13.36	0	0
1B159	7/27/2008	T5	CT	114	17.1	0.52	9.72	0.35	0.52	6.25	0	0
1B162	7/27/2008	T5	CT	170	61.3	4.43	8.23	0.63	17.72	17.72	14.56	0
1B165	7/27/2008	T5	CT	189	74.5	0	0.4	0	13	0	0	0
1B166	7/27/2008	T5	CT	144	35.1	0.22	0	0	0.65	4.52	0	5.38
1B167	7/27/2008	T5	CT	83	8.3	1.29	5.38	2.79	0	0.5	0	0
1B168	7/27/2008	T5	CT	142	30.5	0.85	0.85	1.28	0.43	0	31	8.08

1B170	7/27/2008	T5	CT	117	21.6	1.49	5.96	1.28	0.64	9.59	0	2.34
1B173	7/27/2008	T5	CT	125	20.7	1.28	0.82	5.29	0	0	0	1.73
1B174	7/27/2008	T5	CT	165	52.5	0	2.82	1.41	33.19	14.12	0	19.07
1B175	7/27/2008	T5	CT	96	11.9	1.25	3.75	0	34.98	12.49	0	9.99
1B176	7/27/2008	T5	CT	94	9.8	0	0	0	3.39	8.81	31.86	23.73
1B177	7/27/2008	T5	CT	99	11.1	0.24	0	2.3	0.73	6.3	2.54	0
1B178	7/27/2008	T5	CT	151	22	0.1	1.31	0.14	0	0.38	1.51	0
1B180	7/27/2008	T5	CT	90	7.9	0.42	0.42	0.21	0.21	0	18.18	1.69
1B181	7/27/2008	T5	CT	89	7.3	1.56	1.74	1.39	0	8.51	4.17	0
1B182	7/27/2008	T5	CT	87	9.1	1.31	0.33	4.26	0.66	4.59	13.44	8.2
1B184	7/27/2008	T5	CT	96	10.4	0.07	0.66	2.57	0	3.29	0	0
1B163	7/27/2008	T8	CT	153	39.7	0.35	0	0.23	0	0	10.98	0
1B186	7/29/2008	T8	CT	96	10.1	0.71	0.84	0.67	1.89	0.08	0	0
1B187	7/29/2008	T8	CT	109	14.2	0.13	0	0.29	0.56	0	0.17	0
1B188	7/29/2008	T8	CT	111	15.2	0.39	1.16	0	0	0.39	36.82	0
1B189	7/29/2008	T8	CT	152	39.8	0.17	0.39	0.47	3	0.26	0	0
1B190	7/29/2008	T8	CT	167	55.9	0	54.97	5	1.67	2.5	19.16	0
1B191	7/29/2008	T8	CT	93	9.1	0.13	0	0.24	0	0	0	0
1B192	7/29/2008	T8	CT	88	7.8	0	0	0.2	0	0	0	0
1B193	7/29/2008	T8	CT	90	7.5	1.09	0.11	1.09	0.11	0	8.49	0
1B194	7/29/2008	T8	CT	80	5.8	0	0	0.51	1.81	0	0	0
1B195	7/29/2008	T8	CT	94	9.1	0.2	0.37	0	0	0	0	0
1B196	7/29/2008	T8	CT	97	10.1	0.57	0.81	0.42	0.13	0.26	0	0
1B198	7/29/2008	T8	CT	102	13.2	0.84	7.27	4.2	12.87	2.8	0	0
1B199	7/29/2008	T8	CT	149	34.9	0	0	4.76	54.74	0	19.83	0

1B201	7/29/2008	T8	CT	119	20.2	0.11	5.05	2.18	2.53	1.61	0	0
1B202	7/29/2008	T8	CT	111	15.6	0.17	0.06	0.06	0.87	0.41	0	0
1B203	7/29/2008	T8	CT	92	8.5	0.17	1.51	0.42	0	0	0	0
1B206	7/29/2008	T8	CT	131	23.3	0.05	2.76	0.19	1.47	0.29	0	0
1B207	7/29/2008	T8	CT	86	9.1	0.57	5.95	0	0.14	0.5	0	0
1B208	7/29/2008	T8	CT	86	7	4.8	2.51	3.77	0.34	0	0	0
1B213	7/29/2008	T8	CT	113	14.4	0	2.82	7.24	1.01	0.6	8.45	0
1B153	7/27/2008	UPM	CT	140	27.3	0	1.41	0	0	0	33.89	0
1B155	7/27/2008	UPM	CT	159	44.4	0.24	0.24	0.97	1.7	14.6	0	6.57
1B157	7/27/2008	UPM	CT	170	61.3	0	0	0	2.45	0	120.14	0
1B158	7/27/2008	UPM	CT	84	6.7	0.25	0.51	17.68	2.02	2.02	0	2.78
1B227	7/27/2008	UPM	CT	88	6.6	0.46	0.1	0.04	0.16	0	0	0
1B228	7/27/2008	UPM	CT	90	7.9	0.76	1.66	3.33	1.18	0	0	0
1B229	7/27/2008	UPM	CT	152	38.8	0.03	0	0.39	0	0	0	0
1B230	7/27/2008	UPM	CT	149	31.9	0	9.36	0	0	0.12	2.22	0
1B231	7/27/2008	UPM	CT	99	10.4	0.83	4.2	0	0	0	1.86	0
1B232	7/27/2008	UPM	CT	172	59.3	0	0	0	2.14	2.94	7.21	14.42
1B234	7/27/2008	UPM	CT	155	34.8	0.19	2.73	0	0.78	4.28	11.49	0
1B217	7/27/2008	UPM	CT	90	7.8	0.12	0.24	4.11	1.53	0	0	5.76
1B218	7/27/2008	UPM	CT	93	7.6	0.04	0.77	0.4	0	0	0	0
1B219	7/27/2008	UPM	CT	91	7.3	1.03	0.32	0	0	0	0	0
1B220	7/27/2008	UPM	CT	184	75.3	2.43	0	8.51	45.61	0.61	0	3.65
1B221	7/27/2008	UPM	CT	90	7.6	1.07	0	0.18	0	1.4	0	0.93
1B222	7/27/2008	UPM	CT	87	6.9	1.77	0.47	0	0	0	0	0
1B224	7/27/2008	UPM	CT	141	29.3	0.56	1.68	1.68	2.23	1.49	0	1.68

1B226	7/27/2008	UPM	CT	97	8.4	2.67	0	5.1	0.32	0	0	0
1B103	7/26/2008	T1	SC	64	5.5	0.44	0.013	0.8	0	0	0	0
1B109	7/26/2008	T1	SC	61	5.2	0.21	0	0	0	0	0	0
1B113	7/26/2008	T1	SC	66	6	0	0.77	0.29	0	0	0	0
1B140	7/26/2008	T1	SC	67	7.1	0	0.76	0.09	0	0	0	0
1B144	7/26/2008	T1	SC	66	7.1	3.35	0	1.46	0	0.05	0	0
1B145	7/26/2008	T1	SC	63	5.7	0	0.37	0	0	0	0	0
1B147	7/26/2008	T1	SC	62	5.4	6.74	0	1.48	0	0	0	0
1B150	7/26/2008	T1	SC	68	6.5	0	0.19	2.49	0	0	0	0
1B151	7/26/2008	T1	SC	68	7.5	0	0.08	0.19	0	0	0	0
1B204	7/26/2008	T1	SC	59	4.8	0.03	0.01	0.08	0	0	0	0
1B123	7/27/2008	T5	SC	72	8	0.07	0	0.17	0	2.21	0	0
1B124	7/27/2008	T5	SC	79	11.2	0.08	0.82	1.84	0	0	0	0
1B125	7/27/2008	T5	SC	71	7.9	0.42	0.37	0.97	0	0	0	0
1B126	7/27/2008	T5	SC	71	7.5	0	0	2.29	0	0.02	0	0
1B127	7/27/2008	T5	SC	105	28	0	0	1.1	0	0	0	0
1B129	7/27/2008	T5	SC	79	10.9	0.04	1.18	3	0	0	0	0
1B130	7/27/2008	T5	SC	78	9.5	0	2.27	0.07	0	0.07	0	0
1B131	7/27/2008	T5	SC	86	13.8	0	1.66	1.02	0	0.08	0	0
1B132	7/27/2008	T5	SC	80	10.9	0	0	0.39	0	0	0	0
1B133	7/27/2008	T5	SC	82	12.1	0.5	7.36	0.5	0	0	0	0
1B134	7/27/2008	T5	SC	74	8.7	0	0	0.76	0	0	0	0
1B135	7/27/2008	T5	SC	71	7.5	0	0	1.72	0	0	0	0
1B137	7/27/2008	T5	SC	72	8.4	0.76	0	0.25	0	0	0	0
1B139	7/27/2008	T5	SC	61	5.9	0.29	0.19	1.92	0	0	0	0

1B143	7/27/2008	T5	SC	76	9.8	0	1.5	0.68	0	0	0	0
1B233	7/27/2008	T5	SC	82	11.7	0	0	0	0	0.09	0	0
1B179	7/27/2008	T5	SC	69	6.9	0	2.32	1.19	0	0	0	0
1B183	7/27/2008	T5	SC	79	11.8	0.22	0	21.21	0	0.44	0	0
1B102	7/29/2008	T8	SC	60	4.8	2.15	5.76	1.85	0	0	0	0
1B107	7/29/2008	T8	SC	63	4.9	0.05	0.06	0.04	0	0	0	0
1B197	7/29/2008	T8	SC	68	6.6	0.19	0	0.05	0	0.52	0	0
1B200	7/29/2008	T8	SC	65	6	0.18	0.19	0.2	0	0	0	0
1B205	7/29/2008	T8	SC	58	4.3	0	0.25	0.61	0	0	0	0
1B210	7/29/2008	T8	SC	65	6.6	1.45	1.87	0.41	0	0	0	0
1B211	7/29/2008	T8	SC	63	5.9	0.23	0.76	0.16	0	0	0	0
1B212	7/29/2008	T8	SC	72	8.1	0	0.6	29.36	0	0	0	0
1B214	7/29/2008	T8	SC	66	7.8	0	0.36	0.56	0.66	0	0.97	0
1B215	7/29/2008	T8	SC	69	7.4	0.06	0.06	1.73	0	0	0	0
1B156	7/27/2008	UPM	SC	62	4.9	0.22	0	0.89	0	0.56	1.9	0
1B160	7/27/2008	UPM	SC	58	3.6	0.07	0	0.05	1.6	0	0	0
1B161	7/27/2008	UPM	SC	53	2.8	1.43	0	0	0	0	0	0
1B164	7/27/2008	UPM	SC	65	4.8	1.12	0	1.68	0	0	0	0
1B169	7/27/2008	UPM	SC	62	4.9	1.41	0.46	0.32	0	0.12	0	0
1B171	7/27/2008	UPM	SC	54	3.2	0.08	0	0.4	0	0	0	0
1B172	7/27/2008	UPM	SC	60	3.8	0.13	0	0	0	0	0	0
1B235	7/27/2008	UPM	SC	57	4.9	0.55	0	0.82	0	0	0	0
1B223	7/27/2008	UPM	SC	60	4.6	0.22	0	0	0	0	0	0
1B225	7/27/2008	UPM	SC	61	5	0.06	0	0	0	0	0	0
1C237	9/18/2008	T1	CT	68	3.2	0	0	0.6	0	0	0	6.9



1C248	9/18/2008	T1	CT	103	11.7	0	1.28	0	0.06	4.2	0.06	0.23
1C252	9/18/2008	T1	CT	104	10.6	0.45	0	0.24	1.03	0	0	0
1C255	9/18/2008	T1	CT	91	7.7	0	0	0	51.05	0	0	0
1C261	9/18/2008	T1	CT	68	3.3	0	0	0	0	15.71	0	1.75
1C269	9/18/2008	T1	CT	96	8.8	0.09	0.46	0.08	0	0	0	0
1C273	9/18/2008	T1	CT	65	3.1	0.22	0	1.75	0	0	0	0
1C277	9/18/2008	T1	CT	64	3	0	0	0	0	0	0	0
1C283	9/18/2008	T1	CT	145	27.7	0.22	0	0.07	0.07	3.31	0	0
1C284	9/18/2008	T1	CT	63	2.7	0.02	0	0.05	0	0	0	0
1C294	9/18/2008	T1	CT	64	2.8	0.02	0.23	0	0	0	0	0
1C304	9/18/2008	T1	CT	105	12.3	0	0	0.18	0	17.99	0	0
1C320	9/18/2008	T1	CT	127	20.6	0	0	0.35	0	0	0	0
1C323	9/18/2008	T1	CT	128	23.6	0	0	1.03	1.03	75.95	14.37	11.29
1C328	9/18/2008	T1	CT	121	18.7	0.14	0	0.27	1.3	0	0	0
1C376	9/18/2008	T1	CT	92	7.8	0.02	0.25	0	0	2.19	0	0
1C381	9/18/2008	T1	CT	67	2.8	0.12	0	0.16	0	2.52	0	1.2
1C385	9/18/2008	T1	CT	103	10.8	0.58	0	0	1.04	0	0	0.46
1C266	9/18/2008	T5	CT	72	4.6	0.53	0.95	0.95	0	0.11	0	8
1C267	9/18/2008	T5	CT	74	4.2	0.07	0.43	0	0	2.3	1.01	3.38
1C275	9/18/2008	T5	CT	142	27.9	0	0	0	19	0	0	13.76
1C353	9/18/2008	T5	CT	107	13.5	0.13	0	0	0.18	1.5	0	0
1C360	9/17/2008	T5	CT	102	10.7	0.08	0	0.3	0.41	0	0	0
1C362	9/18/2008	T5	CT	89	7.3	0.06	0	0	0	0	0	0
1C290	9/18/2008	T5	CT	62	2.3	0.57	0.37	1.11	0	0	0	0
1C365	9/18/2008	T5	CT	98	9.1	0.39	0.42	0.74	0	0	0	0

1C369	9/18/2008	T5	CT	107	13	0	0	0.77	0	0	0	4.71
1C372	9/18/2008	T5	CT	115	16.2	0.77	0	0	68.69	7.72	0	0
1C374	9/18/2008	T5	CT	98	9.2	0.12	0.35	0	0.29	0	0	0
1C377	9/18/2008	T5	CT	101	11.7	0	0.14	0	0.83	0	0	12.81
1C378	9/18/2008	T5	CT	116	19.6	0	0	0	1	3.01	0	12.71
1C379	9/18/2008	T5	CT	89	6.5	0	0	0	0	1.09	2.81	0
1C380	9/18/2008	T5	CT	133	22.7	0.16	0	0	0	0	0	1.3
1C382	9/18/2008	T5	CT	102	11.9	0	0	0	0.64	0	0	0
1C384	9/18/2008	T5	CT	108	12.8	0.02	0.11	0	0.25	0.71	0.56	0
1C386	9/18/2008	T5	CT	64	2.8	0.16	0	0	0.22	0	0	0
1C387	9/18/2008	T5	CT	73	4.2	0.07	1.07	0	0.05	0	0	0
1C390	9/18/2008	T5	CT	68	3.3	0	0	0	0	0	0	0
1C242	9/19/2008	T8	CT	156	36.3	0	0	0	0	0.01	0	0
1C245	9/19/2008	T8	CT	120	19.7	0.16	2.23	0	0	0	3.43	2.15
1C249	9/18/2008	T8	CT	158	44	0	3.98	0	0	16.68	0	4.23
1C253	9/19/2008	T8	CT	156	39.3	0	0	0.25	0	0	0	1.7
1C263	9/19/2008	T8	CT	114	16	0.01	0	0	0	0.16	0	0
1C300	9/19/2008	T8	CT	95	9	0	1	0.52	0	0	0	0
1C301	9/19/2008	T8	CT	90	9.1	0.2	0	0	0.2	0	0.1	9.52
1C303	9/19/2008	T8	CT	99	10.4	1.79	0	1.88	0	0.58	0.22	0
1C305	9/19/2008	T8	CT	101	13.2	0.24	0	0.25	0.08	0	0	0
1C308	9/19/2008	T8	CT	132	25.3	0	0	0	3.58	6.65	0	0
1C312	9/19/2008	T8	CT	65	3.1	0.05	0.17	0.01	0	0	0	0
1C315	9/19/2008	T8	CT	75	5.9	0.58	1	0	0	0	0	0
1C318	9/19/2008	T8	CT	63	3.5	0.01	0	0	0	0	0	0

1C319	9/19/2008	T8	CT	112	15.7	0.14	0	0	1.29	0.03	1.29	0
1C322	9/19/2008	T8	CT	63	2.9	0.41	0.11	0	0	0	0	0
1C324	9/19/2008	T8	CT	131	23.6	0.21	0	1.09	0	1.3	0	0
1C326	9/19/2008	T8	CT	85	6.3	0.3	0	0.42	0.17	0.11	0	0
1C327	9/19/2008	T8	CT	86	6.7	0.08	0.15	0.08	0	6.96	0	0.46
1C350	9/17/2008	UPM	CT	91	7.5	0.02	2.18	0.12	0.05	0	0	0
1C351	9/17/2008	UPM	CT	90	6.6	0.41	0.55	0	0.55	12.16	0	0
1C355	9/17/2008	UPM	CT	89	6.8	0.16	1.26	0	0	0.64	0	0
1C356	9/17/2008	UPM	CT	94	9	0.13	2.97	0	0	0.1	0	0
1C357	9/17/2008	UPM	CT	93	7.9	0.26	0	0.77	0.77	11	0	0
1C361	9/17/2008	UPM	CT	98	10	0.6	5.36	0	0.12	0	0	5.84
1C329	9/17/2008	UPM	CT	98	9.6	0.08	1.66	0.17	5.48	0.91	0	0
1C335	9/17/2008	UPM	CT	106	13	1.21	6.64	0	51.33	1.21	0	0
1C336	9/17/2008	UPM	CT	113	15.5	0.21	0.86	0	0	20.41	0	0
1C337	9/17/2008	UPM	CT	103	11.5	0	0.35	0.66	1.52	2.53	0	0
1C338	9/17/2008	UPM	CT	104	12	0	0	0	0	14	0	0
1C339	9/17/2008	UPM	CT	142	27.4	0.03	2.09	0	1.09	0	0	0
1C340	9/17/2008	UPM	CT	100	10.7	1.76	0	0	36.87	43.89	0	5.27
1C341	9/17/2008	UPM	CT	100	10	1.5	0	0.19	0	2.82	4.88	9.39
1C342	9/17/2008	UPM	CT	98	9.5	0	2.94	0	0.2	8.44	8.05	0
1C343	9/17/2008	UPM	CT	92	8	0	0	0	0	0.29	0	0
1C344	9/17/2008	UPM	CT	101	9.8	0	2.74	0	0	0	0	0
1C345	9/17/2008	UPM	CT	126	21.5	0.48	0	0	0.12	11.35	0	0
1C346	9/17/2008	UPM	CT	92	7.1	0.57	0	0.03	0.09	0.85	0	0
1C238	9/18/2008	T1	SC	60	5.2	0.36	0	0.08	0	0	0	0

1C247	9/18/2008	T1	SC	38	4.3	0	0	2.7	0	0	0	0
1C264	9/18/2008	T1	SC	63	4.7	0.04	0.53	0.64	0	0	0	0
1C278	9/18/2008	T1	SC	56	3.9	0	0.42	0	0	0	0	0
1C280	9/18/2008	T1	SC	68	7.3	0.04	0.45	0	0	0.2	0	0
1C288	9/18/2008	T1	SC	58	4.2	0	0	0.92	0	0	21.97	0
1C293	9/18/2008	T1	SC	67	5.8	0	0	1.55	0	0	0.8	0
1C296	9/18/2008	T1	SC	63	5.6	0.01	0	0.74	0	0	0	0
1C389	9/18/2008	T1	SC	62	4.9	0.02	0	2.36	0	0	0	0
1C363	9/18/2008	T5	SC	71	7.4	0	0	5.98	0	0	0	0
1C364	9/18/2008	T5	SC	62	5	0	0.05	0.2	0	0	0	0
1C366	9/18/2008	T5	SC	61	4.6	0.23	0	0	0	0	0	0
1C367	9/18/2008	T5	SC	57	3.6	0.1	0	0.7	0	0	0	0
1C368	9/18/2008	T5	SC	63	7.8	0	0	0.09	0	0	0	0
1C371	9/18/2008	T5	SC	72	7.8	0	0	0.57	0	0	0	0
1C375	9/18/2008	T5	SC	58	4.1	0	0	2.9	0	0	0	0
1C383	9/18/2008	T5	SC	61	4.6	0	0	1.1	0	0	0	0
1C243	9/19/2008	T8	SC	71	8.2	0.14	0	2.16	0	0	0	0
1C299	9/19/2008	T8	SC	67	6.3	0	0	1.93	0	0	0	0
1C307	9/19/2008	T8	SC	71	8	0.93	0	1.9	0.98	0	0.15	1.18
1C311	9/19/2008	T8	SC	68	7.1	0	0	0.58	0	0	0	0
1C316	9/19/2008	T8	SC	75	10.1	0	0	7.1	0	0	0	0
1C325	9/19/2008	T8	SC	74	9.1	0.07	0	0.96	0	0	0	0
1C352	9/17/2008	UPM	SC	59	4.6	0	4.21	0.8	0	0	0	0
1C354	9/17/2008	UPM	SC	55	3.4	1.81	0.97	0.45	0	0	0	0
1C358	9/17/2008	UPM	SC	68	6.3	0.03	0	0.91	0	0	0	0

1C330	9/17/2008	UPM	SC	57	4	0.21	0.06	0	0	0	0	0
1C331	9/17/2008	UPM	SC	61	5	0.11	0	0	0	0	0	0
1C332	9/17/2008	UPM	SC	61	4.3	0.01	0	0	0	0	0	0
1C333	9/17/2008	UPM	SC	70	9	0.36	0	0	0	0	0	0
1C347	9/17/2008	UPM	SC	55	3.9	0.16	1.15	0	0	0	0.15	0
1C348	9/17/2008	UPM	SC	62	5	0.19	0.07	0.01	0	0	0	0
1C349	9/17/2008	UPM	SC	56	3.5	0	0.21	0.87	0	0	0	0

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Table B-3. Raw diet data collected from May 20 to September 19, 2008 with the calculated biomass estimates of major taxonomic orders and other invertebrate categories consumed, Ephemeroptera (Ephem), Plecoptera (Plecop), Trichoptera (Trichop), Diptera, Coleoptera (Cole), Hymenoptera (Hymen) and other invertebrates (OT), sorted by month, consumer class and site.

Season	Consumer Class	Site	Length (mm)	Weight (g)	Ephem (mg)	Plecop (mg)	Trichop (mg)	Diptera (mg)	Cole (mg)	Hymen (mg)	OT (mg)
MAY	CT<100	GUS	98	14	37.67	0.65	22.2	7.57	0	11	0
MAY	CT<100	GUS	88	7.3	10.66	0.48	0	0.7	0	0	0
MAY	CT<100	GUS	76	4.9	0	0	0	0.21	0	0	0
MAY	CT<100	GUS	76	7.4	2.43	6.7	0.008	0.21	0	0	25.6
MAY	CT<100	GUS	69	4.1	1	0	0	1.16	0	0	0
MAY	CT<100	GUS	82	7.6	6.96	0	0	0.38	0	0	0
MAY	CT<100	GUS	96	12.2	4.18	1.1	58.9	28.1	0	0	0
MAY	CT<100	MS	92	9.9	14.56	0	0	0	0	0	0
MAY	CT<100	MS	93	9	28.69	0	5.27	21.52	0	12	0
MAY	CT<100	MS	92	10.4	6.47	0	15.15	1.56	0	0	14.51
MAY	CT<100	MS	88	7.2	8.78	0.08	2.7	18.24	0	0	5.01
MAY	CT<100	MS	60	2.7	0.41	0.13	0	0.1	0	0	0
MAY	CT<100	MS	95	9.3	2.43	0	2.4	0.58	1.1	0	6.63
MAY	CT<100	MS	64	2.8	0.24	0	0	0.29	0	0	0
MAY	CT<100	MS	98	10	5.04	0	12	1.61	0.86	0	4.67
MAY	CT<100	MS	86	7.3	14.99	0	0	0.3	0	0	0
MAY	CT<100	MS	74	4.4	1.08	2.4	0.08	0.08	0	0	0
MAY	CT<100	MS	75	5.5	0.96	0.17	0.13	0.56	0	0	0
MAY	CT<100	MS	91	8.9	12.65	0.25	4.56	1.16	0	0	29.4
MAY	CT<100	MS	92	9.4	15.67	0.39	4.4	4.77	0	0	0
MAY	CT<100	POT	80	6.7	1.48	0.25	0.56	0.18	0	0	0
MAY	CT<100	POT	84	7.8	0	0	1.28	6.4	0	0	0.95

MAY	CT<100	POT	78	6	1.2	0	3.7	0.72	0	0	0
MAY	CT<100	POT	83	7.8	0	0	1.45	2.53	0.04	0	0
MAY	CT<100	POT	76	5.2	5.77	3.9	7.08	0.27	0	0	1.54
MAY	CT<100	POT	76	5.2	4.39	0.02	0	2.22	0	0	1.4
MAY	CT<100	POT	98	11.6	4.91	1.14	18.71	2.2	0.07	12	0
MAY	CT<100	POT	74	5.4	6.02	0.01	0	0.23	0	0	0
MAY	CT<100	POT	99	10.5	2.69	0	7.01	0	0	0	0
MAY	CT<100	POT	98	10.6	17.72	0	1.3	1.85	0	0	0
MAY	CT<100	POT	78	5.8	3.04	0.3	3.08	3.41	1.1	0	0
MAY	CT<100	RCK	81	7.3	13.39	0.4	1.1	0	0	0	11.9
MAY	CT<100	RCK	75	5.1	2.03	4.34	0.03	1.04	0	0	0
MAY	CT<100	RCK	94	9.6	13.71	0	1.11	0.65	0	0	0
MAY	CT<100	RCK	85	8.6	6.51	0	2.44	7.96	0.13	0	1.97
MAY	CT<100	RCK	96	10.5	27.24	0.5	6.68	0.43	0	0	0
MAY	CT<100	RCK	80	7	5.88	0.36		0.07	11.3	0	1.84
MAY	CT<100	RCK	98	10.8	6.79	0	0	6.57	0.14	0	0
MAY	CT<100	RCK	92	9.9	2.34	0	4.6	0.02	7.7	0	3.2
MAY	CT<100	RCK	91	8.6	15	0	1.4	2.45	0	0	1.5
MAY	CT<100	RCK	84	7.7	3.39	0	9.4	0	0	0	0
MAY	CT<100	RCK	99	12	7.52	0.13	2.1	1.2	8.52	0	2.4
MAY	CT>100	GUS	127	23.1	65.3	1.1	38.2	18.49	0	0	3.5
MAY	CT>100	GUS	124	22.4	14.8	2.5	0	0	0	0	0
MAY	CT>100	GUS	155	37	33.54	25.2	25.67	2.34	0	0	0
MAY	CT>100	GUS	110	18	34.6	11.2	12.28	2.99	6.5	0	3
MAY	CT>100	GUS	113	18.9	28.83	0	54.39	28.06	0	0	0
MAY	CT>100	GUS	100	12.8	10.38	0	20.99	3.86	0	0	0.53
MAY	CT>100	MS	134	30.4	2.8	2.5	8.17	0.2	2	0	3.1
MAY	CT>100	MS	107	16.3	14.94	35	9.67	17.78	0	0	5
MAY	CT>100	MS	118	19.8	8.12	0	11.1	0.09	6.9	0	7.27

MAY	CT>100	MS	122	24.8	12.8	1.05	10.67	0	0	0	0
MAY	CT>100	MS	119	20	3.42	0	0.69	0.58	0	0	5.8
MAY	CT>100	MS	102	13	9.4	0	6.51	0.03	0	0	0.63
MAY	CT>100	MS	146	32.2	13.96	3.75	1.99	1.68	0	0	0
MAY	CT>100	MS	129	25.2	10.26	0.33	0	1.16	0	0	0
MAY	CT>100	MS	114	18.6	13.92	0	0.3	3.8	7.1	0	0
MAY	CT>100	POT	104	13.7	23.82	0	2.4	2.03	0	0	0.47
MAY	CT>100	POT	117	21.7	6.01	0	1.42	17	7.2	0	0
MAY	CT>100	POT	114	20.3	4.47	0.41	9.95	4.17	0	0	0
MAY	CT>100	RCK	154	41.3	11.84	3.3	11.65	0.44	3.6	14	6
MAY	CT>100	RCK	106	15.7	9.8	0	0.16	0.12	2.1	0	0.78
MAY	CT>100	RCK	144	38.9	61.96	2.05	12.51	26.36	6	45.1	14.54
MAY	CT>100	RCK	125	24.7	15.28	0	12.01	15.52	5.7	57	4
MAY	CT>100	RCK	101	14.5	2.82	0	0	0	0	0	0
MAY	CT>100	RCK	110	16.7	23.06	0	3.19	0.8	0	0	3.4
MAY	SC	MS	60	4.8	8	0	0	0.26	0	0	0
MAY	SC	MS	69	6.9	9.14	0.24	1.2	0.02	0	0	0
MAY	SC	MS	60	5	2.39	0	0.15	0	0	0	0
MAY	SC	MS	65	5.8	0.23	0.3	0	0.11	0	0	0
MAY	SC	MS	65	6	2.22	0	0	0	0	0	0
MAY	SC	MS	64	5.3	0.68	0.76	0	0	0	0	0
MAY	SC	MS	57	4.2	2.88	0	0	0.02	0	0	0
MAY	SC	POT	56	3.6	0	0	0	0.38	0	0	0
MAY	SC	POT	62	4.9	3.2	0.81	4.6	0.1	0	0	0
MAY	SC	POT	56	3.6	0.37	0.24	0	0.03	0	3.3	0
MAY	SC	POT	57	3.6	0.68	0	4.4	0.08	0	0	0
MAY	SC	POT	65	6.1	0	0.25	0	0.5	0	0	0
MAY	SC	POT	58	12.1	0	0	0.24	0.05	0	0	0
MAY	SC	RCK	69	8.6	0.63	0.06	0	0.79	0	0	0



MAY	SC	RCK	68	7.7	18.31	4.8	3.4	0	0	0	1.2
MAY	SC	RCK	54	4.3	14.78	0.03	0.43	0	0	0	0
MAY	SC	RCK	72	9.8	6.54	23	0	0.09	0	0	0
MAY	SC	RCK	55	4.2	2.56	4.6	7.2	0	0	0	0
MAY	SC	RCK	66	7.8	0.39	0	0	0	0	0	0
MAY	SC	RCK	66	6.5	11.21	0.14	0.08	0.03	0	0	0
MAY	SC	RCK	68	7.6	5.8	0	0	0	0	0	0
MAY	SC	RCK	81	11.5	8.2	0	0.21	12	0	0	0
MAY	SC	RCK	80	10.2	8.72	6.2	2.3	0.07	0	0	0
MAY	SC	RCK	61	4.3	1.07	0	0	0	0	0	0
MAY	SC	RCK	90	17.2	7.34	0	1.3	8.74	0	0	0
MAY	SC	RCK	76	10.2	2.58	0	0	0.05	0	0	0.02
JULY	CT<100	GUS	96	10.1	1.26	2.14	0	0.71	0	0	0.09
JULY	CT<100	GUS	93	9.1	0.24	0	0	0.13	0	0	0
JULY	CT<100	GUS	88	7.8	0.2	0	0	0	0	0	0
JULY	CT<100	GUS	90	7.5	1.07	0	0.14	1.17	8.5	0	0
JULY	CT<100	GUS	80	5.8	0.51	0	1.8	0.01	0	0	0
JULY	CT<100	GUS	94	9.1	0	0	0.37	0.2	0	0	0
JULY	CT<100	GUS	97	10.1	0.26	0.15	0.82	0.71	0	0	0.26
JULY	CT<100	GUS	92	8.5	0.02	0.4	1.51	0.17	0	0	0
JULY	CT<100	GUS	86	9.1	0	0	3.73	1.24	2.2	0	0
JULY	CT<100	GUS	86	7	4.01	0	2.57	4.79	0	0	0
JULY	CT<100	MS	84	6.7	5.06	14.3	0.46	0.59	1.5	2.9	0.45
JULY	CT<100	MS	90	7.8	4.12	0	1.75	0.08	0	5.8	0
JULY	CT<100	MS	93	7.6	0.39	0	0.78	0.04	0	0	0
JULY	CT<100	MS	91	7.3	0.01	0	0.32	1.02	0	0	0
JULY	CT<100	MS	90	7.6	0	0.17	0	1.08	0	0.93	1.4
JULY	CT<100	MS	87	6.9	0	0	0.46	1.78	0	0	0
JULY	CT<100	MS	97	8.4	1.46	3.66	0	2.97	0	0	0

JULY	CT<100	MS	88	6.6	0.04	0	0.1	0.62	0	0	0
JULY	CT<100	MS	90	7.9	2.63	0.7	1.64	1.78	0	0	0
JULY	CT<100	MS	99	10.4	0	0	4.18	0.86	1.85	0	0
JULY	CT<100	POT	95	9.4	1.83	0	2.77	0.85	15	0	2.1
JULY	CT<100	POT	94	8.8	0.23	0	0	0	36	0	0
JULY	CT<100	POT	98	10.3	0.5	0.41	1.53	4.88	20	1.7	0.17
JULY	CT<100	POT	96	10.9	0.21	0	0	0	0	0	0
JULY	CT<100	POT	91	10.3	4.77	0.35	0.66	0.77	0	0	16
JULY	CT<100	POT	87	8.2	2.32	0	1.77	1.9	0	0	0.8
JULY	CT<100	POT	94	9.2	0.06	2.49	0	0.34	0	0	0
JULY	CT<100	POT	94	8.7	0.37	9.4	0	0.05	0	0	0
JULY	CT<100	POT	95	10.8	0.31	0	1.39	0.26	0	0	0
JULY	CT<100	RCK	88	7.7	0	0	0.18	7.4	0	2.7	2.04
JULY	CT<100	RCK	83	8.3	2.74	0.04	1.01	1.29	0.49	0	4.4
JULY	CT<100	RCK	96	11.9	0	34	1.1	1.46	4.4	9.7	8.4
JULY	CT<100	RCK	94	9.8	1.67	0	0	2.22	31.7	23.5	8.7
JULY	CT<100	RCK	99	11.1	0.23	2.1	0	0.98	2.56	0	6.25
JULY	CT<100	RCK	90	7.9	0.14	0.1	0.42	0.77	181	1.6	0
JULY	CT<100	RCK	89	7.3	1.47	0	1.67	1.53	7.9	0	4.8
JULY	CT<100	RCK	87	9.1	2.8	1.82	0.38	1.35	16.72	8.2	1.5
JULY	CT<100	RCK	96	10.4	2.57	0	0.64	0.27	0	0	3.1
JULY	CT>100	GUS	153	39.7	0.18	0	0	0.38	11	0	0
JULY	CT>100	GUS	109	14.2	0.28	0	0	0.68	0.18	0	0
JULY	CT>100	GUS	111	15.2	0	0	0.97	0.49	37.3	0	0
JULY	CT>100	GUS	152	39.8	2.28	0	1.47	0.52	0	0	0
JULY	CT>100	GUS	167	55.9	0	5.16	0.46	0.48	19.4	0	57.8
JULY	CT>100	GUS	102	13.2	3.85	13.31	7.23	0.85	0	0	2.73
JULY	CT>100	GUS	149	34.9	7.76	51.19	0	0.25	20.13	0	0
JULY	CT>100	GUS	119	20.2	2.63	0	7.08	0.16	0	0	1.6

JULY	CT>100	GUS	111	15.6	0.48	0	0.51	0.6	0	0	0
JULY	CT>100	GUS	131	23.3	1.07	0	2.75	0.93	0	0	0
JULY	CT>100	GUS	113	14.4	8.03	0	2.28	0.23	8.94	0	0.63
JULY	CT>100	MS	140	27.3	0	0	1.3	0	34	0	0
JULY	CT>100	MS	159	44.4	2.26	0	0.17	0.82	0.01	6.5	14.58
JULY	CT>100	MS	170	61.3	0	0	2.3	0.3	120	0	0
JULY	CT>100	MS	184	75.3	15.93	36.91	0.14	3.42	0	3.6	0.93
JULY	CT>100	MS	141	29.3	2.45	0	1.72	1.95	1.2	1.7	0.29
JULY	CT>100	MS	152	38.8	0.39	0	0	0.03	0	0	0
JULY	CT>100	MS	149	31.9	0	0	9.41	0	2.2	0	0.9
JULY	CT>100	MS	172	59.3	0	0	1.69	0.69	7.1	14.43	2.8
JULY	CT>100	MS	155	34.8	0.34	0	0.1	0.59	14.1	0	4.34
JULY	CT>100	POT	106	12	0.1	0	0.71	1.91	0	0	0.31
JULY	CT>100	POT	103	14.3	0.2	0	0.19	0.24	0	0	0
JULY	CT>100	POT	112	16.4	0.39	0	0	13.27	5	1.7	0.78
JULY	CT>100	POT	106	12.8	2.47	1.1	0	1.08	2.5	0	0.16
JULY	CT>100	POT	121	17	3.29	0	0	2.29	0	7.2	5.2
JULY	CT>100	POT	107	17	0.04	0	0	0.1	0	0	0
JULY	CT>100	POT	120	22.4	0.001	0	3.18	1.96	20.13	0	0.74
JULY	CT>100	POT	108	13.2	3.03	0	0.37	0.82	20.32	0.72	0.38
JULY	CT>100	RCK	132	29	0.86	17.1	2.38	0.04	13.5	0	0
JULY	CT>100	RCK	114	17.1	0.4	0	9.68	0.99	0	0	6.3
JULY	CT>100	RCK	170	61.3	0	13.02	9.07	4.31	19.3	0	17.6
JULY	CT>100	RCK	189	74.5	0	13	0.37	0.03	0	0	0
JULY	CT>100	RCK	144	35.1	0	0	0.65	0.2	0	5.4	4.5
JULY	CT>100	RCK	142	30.5	1.28	0	1.16	0.92	31.2	7.98	0
JULY	CT>100	RCK	117	21.6	0.99	0.76	5.95	1.76	5	7.3	4.54
JULY	CT>100	RCK	125	20.7	0.65	4.7	0.83	1.24	0	1.7	0
JULY	CT>100	RCK	165	52.5	1.39	33	2.92	0.42	7.9	19.1	9.09

JULY	CT>100	RCK	151	22	0.16	0	1.3	0.15	2.4	0	0.34
JULY	SC	GUS	60	4.8	0.96	0.91	5.71	2.18	0	0	0
JULY	SC	GUS	63	4.9	0.04	0	0.06	0.05	0	0	0
JULY	SC	GUS	68	6.6	0.04	0	0	0.71	0	0	0
JULY	SC	GUS	65	6	0.2	0	0.19	0.18	0	0	0
JULY	SC	GUS	58	4.3	0.61	0	0.25	0	0	0	0
JULY	SC	GUS	65	6.6	0.4	0	1.86	1.47	0	0	0
JULY	SC	GUS	63	5.9	0.16	0	0.76	0.23	0	0	0
JULY	SC	GUS	72	8.1	0	29.51	0.45	0	0	0	0
JULY	SC	GUS	66	7.8	1.22	0	0.36	0	0.97	0	0
JULY	SC	GUS	69	7.4	1.74	0	0.05	0.05	0	0	0
JULY	SC	MS	62	4.9	0.9	0	0	2.22	2.46	0	0
JULY	SC	MS	58	3.6	1.64	0	0	0.08	0	0	0
JULY	SC	MS	53	2.8	0	0	0	1.43	0	0	0
JULY	SC	MS	65	4.8	1.68	0	0	1.12	0	0	0
JULY	SC	MS	62	4.9	0.32	0	0.47	1.41	0.11	0	0
JULY	SC	MS	54	3.2	0.39	0	0	0.09	0	0	0
JULY	SC	MS	60	3.8	0	0	0	0.13	0	0	0
JULY	SC	MS	60	4.6	0	0	0	0.22	0	0	0
JULY	SC	MS	57	4.9	0.82	0	0	0.55	0	0	0
JULY	SC	POT	64	5.5	0.8	0	0.01	0.44	0	0	0
JULY	SC	POT	61	5.2	0.21	0	0	0	0	0	0
JULY	SC	POT	66	6	0.03	0.26	0.77	0	0	0	0
JULY	SC	POT	67	7.1	0.09	0	0.76	0	0	0	0
JULY	SC	POT	66	7.1	1.45	0	0	3.41	0	0	0
JULY	SC	POT	63	5.7	0	0	0.37	0	0	0	0
JULY	SC	POT	62	5.4	1.44	0	0	6.78	0	0	0
JULY	SC	POT	68	6.5	2.5	0	0.18	0	0	0	0
JULY	SC	POT	68	7.5	0.19	0	0.08	0	0	0	0

JULY	SC	POT	59	4.8	0.08	0	0.01	0.03	0	0	0
JULY	SC	RCK	72	8	0.18	0	0	0.7	2.2	0	0
JULY	SC	RCK	79	11.2	1.85	0	0.81	0.08	0	0	0
JULY	SC	RCK	71	7.9	0.98	0	0.37	0.42	0	0	0
JULY	SC	RCK	71	7.5	2.3	0	0	0.02	0	0	0
JULY	SC	RCK	105	28	1.1	0	0	0	0	0	0
JULY	SC	RCK	79	10.9	2.51	0.5	1.18	0.03	0	0	0
JULY	SC	RCK	78	9.5	0.08	0	2.28	0	0	0	0.06
JULY	SC	RCK	86	13.8	1.02	0	1.65	0	0	0	0.09
JULY	SC	RCK	80	10.9	0.39	0	0	0	0	0	0
JULY	SC	RCK	82	12.1	0.47	0	7.36	0.53	0	0	0
JULY	SC	RCK	74	8.7	0.76	0	0	0	0	0	0
JULY	SC	RCK	71	7.5	1.72	0	0	0	0	0	0
JULY	SC	RCK	72	8.4	0.25	0	0	0.76	0	0	0
JULY	SC	RCK	61	5.9	1.93	0	0.18	0.28	0	0	0
JULY	SC	RCK	76	9.8	1.7	0	1	0	0	0	0
JULY	SC	RCK	69	6.9	1.2	0	2.34	0	0	0	0
JULY	SC	RCK	79	11.8	0.2	21	0	0.15	0	0	0.52
JULY	SC	RCK	82	11.7	0	0	0	0	0	0	0.09
SEPT	CT<100	GUS	95	9	0.52	0	1	0	0	0	0
SEPT	CT<100	GUS	90	9.1	0	0	0	0.42	0.1	9.5	0
SEPT	CT<100	GUS	99	10.4	0.98	0.88	0.01	1.77	0.23	0	0.61
SEPT	CT<100	GUS	65	3.1	0.01	0	0.17	0.05	0	0	0
SEPT	CT<100	GUS	75	5.9	0	0	0	0.59	0.99	0	0
SEPT	CT<100	GUS	63	3.5	0	0	0.01	0.01	0	0	0
SEPT	CT<100	GUS	63	2.9	0	0	0.11	0.41	0	0	0
SEPT	CT<100	GUS	85	6.3	0.42	0	0	0.58	0	0	0
SEPT	CT<100	GUS	86	6.7	0.01	0.06	0.13	0.08	0	0.47	7
SEPT	CT<100	MS	98	9.6	0.2	5.5	1.67	0.02	0.91	0	0

SEPT	CT<100	MS	98	9.5	0	0	0.04	0.31	15.4	0	3.88
SEPT	CT<100	MS	92	8	0	0	0	0	0	0	0.29
SEPT	CT<100	MS	92	7.1	0.03	0	0	0.66	0	0	0.85
SEPT	CT<100	MS	91	7.5	0	0.1	2.24	0.03	0	0	0
SEPT	CT<100	MS	90	6.6	0	0.09	0.89	0.48	0	0	12.2
SEPT	CT<100	MS	89	6.8	0	0	1.26	0.28	0	0	0.52
SEPT	CT<100	MS	94	9	0	0	2.98	0.2	0	0	0
SEPT	CT<100	MS	93	7.9	0	0.76	0.71	0.32	0	0	11
SEPT	CT<100	MS	98	10	0	0	5.38	0.64	0	5.9	0
SEPT	CT<100	POT	68	3.2	0.03	0.59	0	0	0	6.88	0
SEPT	CT<100	POT	91	7.7	0	51	0	0.05	0	0	0
SEPT	CT<100	POT	68	3.3	0	0	0	0	0	1.66	15.79
SEPT	CT<100	POT	96	8.8	0.08	0	0.46	0.09	0	0	0
SEPT	CT<100	POT	65	3.1	0.99	0.76	0	0.22	0	0	0
SEPT	CT<100	POT	64	3	0	0	0	0.05	0	0	0
SEPT	CT<100	POT	63	2.7	0.05	0	0	0.02	0	0	0
SEPT	CT<100	POT	64	2.8	0	0	0.23	0	0	0	0.02
SEPT	CT<100	POT	92	7.8	0	0	0.24	0.02	0	0	2.2
SEPT	CT<100	POT	67	2.8	0.19	0	0	0.13	0	1.18	2.5
SEPT	CT<100	RCK	72	4.6	0	1	0.93	0.5	0	8	0.09
SEPT	CT<100	RCK	74	4.2	0	0	0.12	0.07	1.32	3.4	2.3
SEPT	CT<100	RCK	62	2.3	0.11	1	0.36	0.58	0	0	0
SEPT	CT<100	RCK	89	7.3	0	0	0	0.06	0	0	0
SEPT	CT<100	RCK	98	9.1	0	0.73	0.42	0.39	0	0	0
SEPT	CT<100	RCK	98	9.2	0	0	0.64	0.12	0	0	0
SEPT	CT<100	RCK	89	6.5	0	0	0	0	2.8	0	1.1
SEPT	CT<100	RCK	64	2.8	0	0	0	0.47	0	0	0
SEPT	CT<100	RCK	73	4.2	0	0	1.07	0.12	0	0	0
SEPT	CT<100	RCK	68	3.3	0.12	0	0	0	0	2.5	0

SEPT	CT>100	GUS	156	36.3	0	0	0	0.01	0	0	0
SEPT	CT>100	GUS	120	19.7	0	0	0	0.16	5.7	2.12	0
SEPT	CT>100	GUS	158	44	0	0	0	0	4	4.3	16.6
SEPT	CT>100	GUS	156	39.3	0	0.25	0	0	0	1.7	0
SEPT	CT>100	GUS	114	16	0	0	0	0.17	0	0	0
SEPT	CT>100	GUS	101	13.2	0	0.25	0	0.31	0	0	0
SEPT	CT>100	GUS	132	25.3	0	3.6	0	0	0	0	6.63
SEPT	CT>100	GUS	112	15.7	0	0	1.3	0.15	1.3	0	0
SEPT	CT>100	GUS	131	23.6	0	1.1	0	0.2	0	0	1.3
SEPT	CT>100	MS	106	13	0	6.2	51.83	1.35	0	0	1
SEPT	CT>100	MS	113	15.5	0.03	0	0	0.44	0.92	0	20.09
SEPT	CT>100	MS	103	11.5	2.11	0	0.44	0	0	0	2.5
SEPT	CT>100	MS	104	12	0	0	0	0	0	0	14
SEPT	CT>100	MS	142	27.4	0	0	3.2	0.02	0	0	0
SEPT	CT>100	MS	100	10.7	0	0	37.22	1.34	0	5.63	43.59
SEPT	CT>100	MS	100	10	0.2	0	0	1.4	4.8	9.4	2.98
SEPT	CT>100	MS	101	9.8	0	0	2.74	0	0	0	0
SEPT	CT>100	MS	126	21.5	0	0	0	0.65	0	0	11.3
SEPT	CT>100	POT	103	11.7	0	0	1.25	0.13	0.02	0.25	4.2
SEPT	CT>100	POT	104	10.6	0.23	0	0.77	0.7	0	0	0.02
SEPT	CT>100	POT	145	27.7	0.08	0	0	0.3	0	0	3.3
SEPT	CT>100	POT	105	12.3	0.11	0	0	0.06	0	0	18.01
SEPT	CT>100	POT	127	20.6	0	0.35	0	0	0	0	0
SEPT	CT>100	POT	128	23.6	0	0.41	0.6	0.26	14	11.2	76.17
SEPT	CT>100	POT	121	18.7	0	0.28	1.3	0.13	0	0	0
SEPT	CT>100	POT	103	10.8	0	0.59	0.71	0.32	0	0.46	0
SEPT	CT>100	RCK	142	27.9	0	0	19	0.05	0	13.7	0
SEPT	CT>100	RCK	107	13.5	0	0	0	1.81	0	0	0
SEPT	CT>100	RCK	102	10.7	0.71	0	0	0.08	0	0	0

SEPT	CT>100	RCK	107	13	0.77	0	0	0	0	4.7	0
SEPT	CT>100	RCK	101	11.7	0.8	0	0.15	0.02	0	12.8	0
SEPT	CT>100	RCK	116	19.6	0.77	0	0.17	0.03	0	12.7	3.05
SEPT	CT>100	RCK	133	22.7	0	0	0	0.16	0	1.3	0
SEPT	CT>100	RCK	102	11.9	0	0	0	0.64	0	0	0
SEPT	CT>100	RCK	108	12.8	0.24	0	0.11	0.02	0.56	0	0.71
SEPT	SC	GUS	71	8.2	2.09	0.09	0	0.13	0	0	0
SEPT	SC	GUS	67	6.3	1.93	0	0	0	0	0	0
SEPT	SC	GUS	71	8	0.77	1.1	0.97	0.93	0.17	1.2	0
SEPT	SC	GUS	68	7.1	0	0.58	0	0	0	0	0
SEPT	SC	GUS	75	10.1	7.04	0.05	0	0	0	0	0
SEPT	SC	GUS	74	9.1	0	0.96	0	0.07	0	0	0
SEPT	SC	MS	57	4	0	0	0.06	0.21	0	0	0
SEPT	SC	MS	61	5	0	0	0	0.12	0	0	0
SEPT	SC	MS	61	4.3	0	0	0.02	0	0	0	0
SEPT	SC	MS	70	9	0	0	0	0.36	0	0	0
SEPT	SC	MS	55	3.9	0	0	1.15	0.16	0.14	0	0
SEPT	SC	MS	62	5	0	0	0.07	0.25	0	0	0
SEPT	SC	MS	56	3.5	0	0.87	0.21	0	0	0	0
SEPT	SC	MS	59	4.6	0	0.81	4.2	0	0	0	0
SEPT	SC	MS	55	3.4	0.46	0	0.97	1.8	0	0	0
SEPT	SC	MS	68	6.3	0.15	0.76	0	0.03	0	0	0
SEPT	SC	POT	60	5.2	0.08	0	0	0.36	0	0	0
SEPT	SC	POT	38	4.3	1.94	0.76	0	0	0	0	0
SEPT	SC	POT	63	4.7	0.64	0	0.53	0.04	0	0	0
SEPT	SC	POT	56	3.9	0	0	0.42	0	0	0	0.01
SEPT	SC	POT	68	7.3	0	0	0.45	0.04	0	0	0.2
SEPT	SC	POT	58	4.2	0	0.89	0	0	22	0	0
SEPT	SC	POT	67	5.8	0.87	0.68	0	0	0.81	0	0



SEPT	SC	POT	63	5.6	0.41	0.33	0	0.01	0	0	0
SEPT	SC	POT	62	4.9	0	2.36	0.01	0	0	0	0.01
SEPT	SC	RCK	71	7.4	0.09	5.89	0	0	0	0	0
SEPT	SC	RCK	62	5	0	0.2	0.05	0	0	0	0
SEPT	SC	RCK	61	4.6	0	0	0	0.23	0	0	0
SEPT	SC	RCK	57	3.6	0.7	0	0	0.1	0	0	0
SEPT	SC	RCK	63	7.8	0	0.09	0	0	0	0	0
SEPT	SC	RCK	72	7.8	0.16	0.41	0	0	0	0	0
SEPT	SC	RCK	58	4.1	0	2.9	0.02	0	0	0	0
SEPT	SC	RCK	61	4.6	0	1.1	0	0	0	0	0

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Appendix C—Pairwise comparisons of rarefied species richness data

Table C-1. Pairwise comparisons of individually rarefied prey abundance levels for May (M), July (J), and September (S) for small cutthroat trout (CT < 100), large cutthroat trout (CT > 100) and cottids (SC). Comparisons are depicted as row vs. column format with (<) or (>) indicating which month/species/size class was rarefied to based on the lowest abundance level for each comparison.

	MSC	MCT<100	MCT>100	JSC	JCT<100	JCT>100	SSC	SCT<100	SCT>100
MSC		< (200)	< (200)	< (200)	< (200)	< (200)	> (130)	< (200)	> (130)
MCT<100	< (200)		> (520)	> (540)	< (580)	< (580)	> (130)	> (240)	> (130)
MCT>100	< (200)	> (520)		< (520)	< (520)	< (520)	> (130)	> (240)	> (130)
JSC	< (200)	> (540)	< (520)		< (540)	< (540)	> (130)	> (240)	> (130)
JCT<100	< (200)	< (580)	< (520)	< (540)		> (680)	> (130)	> (240)	> (130)
JCT>100	< (200)	< (580)	< (520)	< (540)	> (680)		> (130)	> (240)	> (130)
SSC	> (130)	> (130)	> (130)	> (130)	> (130)	> (130)		< (130)	130
SCT<100	< (200)	> (240)	> (240)	> (240)	> (240)	> (240)	< (130)		> (130)
SCT>100	> (130)	> (130)	> (130)	> (130)	> (130)	> (130)	130	> (130)	

Appendix D—Bioenergetic input data

Table D-1. Bioenergetic modeling input data: the mean proportion of functional groups per consumer class with their associated mean mass for the first day and last days of the model simulation.

Consumer Class	Day	Mass of fish (g)	Soft larvae	Rigid Larvae	Aquatic Nymphs	Aquatic Adults	Other Terrestrial	Coleopteran adults	Hymenoptera Adults
Cottids	1	6.77	0.25	0.23	0.42	0.03	0.06	0.02	0.00
CT > 100 mm	1	19.82	0.10	0.15	0.13	0.17	0.15	0.23	0.07
CT < 100 mm	1	8.51	0.16	0.21	0.21	0.11	0.13	0.13	0.05
Cottids	59	7.07	0.23	0.15	0.56	0.00	0.02	0.04	0.00
CT > 100 mm	59	20.35	0.05	0.07	0.08	0.23	0.35	0.05	0.17
CT < 100 mm	59	8.77	0.18	0.25	0.12	0.08	0.21	0.03	0.13

Table D-2. Parameter values for prickly sculpin estimated from consumption and respiration experiments (Moss 2001).

Functions used in Wisconsin Model	Parameter description	Nominal value
<b>Consumption</b>		
CA	Intercept: $C_{\max}^{-1} (\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1})$	0.2325
CB	Coefficient: $C_{\max}$ versus weight	-0.514
CQ	Temperature for $K_1$ ( $^{\circ}\text{C}$ )	6
CTO	Temperature for $K_2$ ( $^{\circ}\text{C}$ )	18
CTM	Temperature for $K_3$ ( $^{\circ}\text{C}$ )	18
CTL	Temperature for $K_4$ ( $^{\circ}\text{C}$ )	24
CK1	Proportion of peak $C_{\max}$ at CQ	0.1075
CK4	Proportion of peak $C_{\max}$ at CTL	0.8129
<b>Respiration</b>		
RA	Intercept: $R (\text{g O}_2/\text{d})$	0.0021
RB	Coefficient: $R$ versus weight	-0.1240
RQ	Coefficient: $R$ versus temperature	0.0616
SDA	Proportion: assimilated energy lost to digestion	0.175
<b>Egestion and Excretion</b>		
FA	Constant proportion of consumption	0.16
UA	Constant proportion of assimilated energy	0.10

Table D-3. Parameter values for rainbow trout estimated from consumption and respiration experiments (Hanson et. al 1997 and references therein).

Functions used in Wisconsin Model	Parameter description	Nominal value
<b>Consumption</b>		
CA	Intercept: $C_{\max}^{-1} (\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1})$	0.628
CB	Coefficient: $C_{\max}$ versus weight	-0.3
CQ	Temperature for $K_1$ ( $^{\circ}\text{C}$ )	5
CTO	Temperature for $K_2$ ( $^{\circ}\text{C}$ )	20
CTM	Temperature for $K_3$ ( $^{\circ}\text{C}$ )	20
CTL	Temperature for $K_4$ ( $^{\circ}\text{C}$ )	24
CK1	Proportion of peak $C_{\max}$ at CQ	0.33
CK4	Proportion of peak $C_{\max}$ at CTL	0.2
<b>Respiration</b>		
RA	Intercept: $R (\text{g O}_2/\text{d})$	0.0026
RB	Coefficient: R versus weight	-0.217
RQ	Coefficient: R versus temperature	0.068
SDA	Proportion: assimilated energy lost to digestion	0.172
<b>Egestion and Excretion</b>		
FA	Constant proportion of consumption	0.212
UA	Constant proportion of assimilated energy	0.0314

